The Role of Invasion Status and Taxon of Basibionts in Marine Community Structure

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Studies on non-native epibionts typically focus on the organismal-level impacts of epibiosis on basibionts, rather than community-level impacts of this relationship. The purpose of our study was to evaluate if non-native basibionts in general facilitate invasions through epibiosis in Maine compared to native basibiont species. We collected 64 basibiont assemblages including replicate samples of 10 different basibiont taxa on the central Maine coast in October 2019. Each basibiont and associated epibionts were identified to genus, classified as native or non-native to the region where they were collected, and weighed. We found that while there was no association between invasion status of the epibiont and the basibiont, native basibionts had a significantly higher Shannon Diversity Index than non-native basibionts. Although diversity of epibionts was greater on native basibionts, the percentage of invaders varied across basibiont taxa. Specific basibiont taxon characteristics may be more important than status because different taxa have different surface topographies, resulting in varying settlement among epibiont species. Our study indicates that there is differential settlement of epibiont taxa across basibiont taxa, which may help predict, based on surface characteristics, which species support more epibiont taxa. This study, as a snapshot of floating dock fouling communities within a 10 km radius, may indicate that non-native basibionts play a role in changing community structure. Expanding the scope of this initial study to include a wider taxonomic and geographic range should help determine if epibiosis is truly a facilitative process in invasions.

Keywords: invasive species, community ecology, epibiosis, biodiversity, basibiont, facilitation

INTRODUCTION

Novel ecosystems are the product of new combinations of native and non-native species, resulting in potential changes in ecosystem functions. These are the result of anthropogenic activity – intentional or inadvertent – and result from degradation or invasion of native ecosystems (Hobbs et al., 2006). Non-native species are a threat to marine biodiversity, and invasions have been found in over 84% of marine ecoregions (Molnar et al., 2008). Regions with low diversity may be at a higher risk for invasion, as well as regions with high numbers of transport vectors or disturbances (Cohen and Carlton, 1998).

A potential facilitative mechanism for invasions that has not been directly examined in the literature is epibiosis. Epibiosis occurs when basibionts, organisms that provide a habitable surface, are colonized by epibionts, the organisms that settle on basibiont surfaces (Wahl, 1989). In the Gulf of Maine, a non-native epibiont *Membranipora membranacea* indirectly facilitates the invasion by *Codium fragile* as the epibiont causes decreased growth and increased mortality in native kelp, a competitor for space, on which the bryozoan settles (Levin et al., 2002). Floerl et al. (2004) described the entrainment of propagules of other species by a non-native bryozoan on the hull of a boat covered in antifouling paint. The bryozoans provided an additional habitable space not otherwise available on the boat surface. Prenter et al. (2004) suggest that such facilitative interspecific interactions increase the success and impact of non-native species. However, there are few studies that look at the community-wide impacts of epibiosis, particularly whether epibiosis is a mechanism for facilitating invasion.

The purpose of this study is to analyze the impact of non-native species in marine ecosystems by focusing on invasion status, taxonomy, and frequency of associated epibionts on basibiont specimens at one location on the central coast of Maine. We aim to determine if facilitation *via* epibiosis is impacting community structure in a marine ecosystem in the Gulf of Maine. We ask if the invasion status of the basibiont impacts the frequency of settled non-native epibionts and if there are any differences in epibiont diversity on native and non-native basibionts. Our predictions are that, if non-native basibionts directly facilitate further invasion, we expect to see an increased frequency of non-native epibiont settlement on non-native basibionts. Because patterns in marine communities suggest there is a relationship between invasion and diversity (Stachowicz et al., 2002), we also predict that there may be a difference in species diversity on non-native basibionts versus native basibionts.

MATERIALS AND METHODS

Study Sites

The samples (n = 64) used in this study were collected from floating docks at three sites in the Damariscotta estuary of Maine on October 11, 2019: a scallop farm at Peter's Island (43°54′32.68″ N, 69°34′05.05″ W), South Bristol Fishermen's Co-op (43°51′50.07″ N, 69°33′16.67″ W), and the Darling Marine Center (43°56′3.16″ N, 69°34′46.41″ W; **Figure 1**).

Collection and Processing of Samples

Each sample consisted of a single basibiont and all associated epibionts. The basibionts were haphazardly selected and removed from the floating docks by hand or by gently scraping the dock surface with a net (mesh size = 4.8 mm). Epibionts were considered any sessile species attached to the basibiont at time of collection. Each sample was placed in a numbered 50 mL polystyrene vial and preserved initially in 99% isopropyl alcohol with menthol crystals for relaxation. In the laboratory, the samples were placed in 70% ethanol for longer preservation.

For each sample, all basibiont and epibiont specimens were identified to genus using dichotomous keys (e.g., Weiss, 1995) and classified by invasion status (native, including cryptogenic taxa if present, or non-native). The blotted wet weight of each basibiont and associated epibionts were individually determined, in addition to the number of epibionts in each sample. We used blotted wet weight as it is a reliable method for estimating size of most common invertebrates (Ricciardi and Bourget, 1998). To ensure reliability of our measurements, we repeated blotting and weighing until the weights of each sample were consistent. We calculated the Shannon Diversity Index (SDI) of the epibiont assemblages on each basibiont, using weight to measure abundance of the organisms as it applies to both colonial and solitary organisms.

Statistical Methods

In our statistical analyses, we pooled the data across all three sites, because these sites were in close proximity (all within 10 km of one another) and had similar fouling communities. We used a chi-square test to determine if there was an association between epibiont and basibiont status using the proportion of non-native organisms in each sample. A t-test was conducted to determine if the percentage of epibionts that were non-native differed among epibionts by their basibiont host status. An additional t-test was used to compare the mean number of epibiont taxa per basibiont genus on native and non-native basibionts to determine if different genera of basibionts supported varying number of taxa.

Four analysis of variance (ANOVA) tests were used to compare across basibiont taxa. First, we compared the epibiont-basibiont weight ratio among basibiont phyla. The second and third ANOVA tests were used to compare the percentage of epibionts that were non-native among basibiont phyla and basibiont genera, respectively. Finally, we compared the SDI of epibionts (by weight) across basibiont phyla. Significant values ($P < 0.05$) were further examined with a Tukey's test.

Finally, we used an analysis of covariance to test the combined effects of basibiont weight and status on each of the following: the percentage of epibionts that were non-native on each basibiont, and the total epibiont weight on each basibiont host. All statistical analyses were conducted in R (R Project for Statistical Computing, SCR_001905).

RESULTS

A total of 64 basibiont assemblages were collected across all sites; 26 basibionts were non-native species, and 38 basibionts were native. The basibionts and epibionts, as well as their associations, are shown in **Table 1**.

Does Invasion Status Matter?

We tested the hypothesis that there is an overall general difference in epibiont characteristics between native and non-native basibionts. Non-native epibionts were equally distributed among native and non-native basibionts (chi-squared = 1.934, df = 1, p = 0.1643). On native basibionts, there were 63 occurrences of non-native epibionts and 37 occurrences of native

FIGURE 1 | Map of study sites in the Damariscotta Estuary. Inset map shows the general location of the sites in the Gulf of Maine, indicated by the pointer symbol.

epibionts. Overall, there were 27 occurrences of each non-native and native epibionts on non-native basibionts (**Figure 2**). Of non-native epibionts, 30% settled on non-native basibionts, and 70% settled on native basibionts.

Quantity, by weight, of non-native epibionts on non-native basibionts (68.988 ± 8.48%) and on native basibionts (69.303 ± 6.09%) were not significantly different in our study ($t = 0.03$, df = 48.6, $P = 0.976$; **Figure 3A**). Native basibiont genera yielded significantly greater epibiont diversity (SDI: 0.296 ± 0.064) than on non-native basibiont genera (SDI: 0.540 ± 0.054; $t = -2.9081$, df = 54.658, $P < 0.01$; **Figure 3B**).

There was no significant difference between mean number of epibiont genera on each native basibiont genus (8.67 ± 2.42) than on non-native basibiont groups (5.00 ± 1.58; $t = -1.269$, df = 7.81, $P = 0.241$; **Figure 3C**). There was also no significant difference in

the epibiont-basibiont weight ratio when comparing non-native (0.929 ± 0.169) to native (1.833 ± 0.483) basibionts ($t = -1.77$, df = 45.655, $P = 0.084$; **Figure 3D**).

Does the Basibiont Taxon Matter?

Cumulatively, molluscan basibionts supported the most epibiont phyla ($n = 7$). Following that were Chordata and Rhodophyta ($n = 5$ each), Ochrophyta ($n = 4$), and Bryozoa ($n = 2$). Only molluscan basibionts supported all of the observed epibiont phyla; and mollusks were the only substrate for arthropod and cnidarian epibionts. However, note that there were varying number of samples for each basibiont phylum (**Table 1**). Chordate epibionts dominated the percent occurrence on all basibiont phyla ($n = 47.54 ± 8.85\%$), followed by molluscan epibionts ($n = 28.40 ± 3.41\%$).

TABLE 1 | The occurrences of epibionts and basibionts collected in this study.

		Phylum Bryozoa	Phylum Chordata				Phylum Mollusca	Phylum Ochrophyta			Phylum Rhodophyta	
		Bugula (n = 2)	*Ciona* (n = 11)	*Didemnum* (n = 2)	*Molgula* (n = 1)	*Styela* (n = 12)	*Mytilus* (n = 14)	*Ascophyllum* (n = 2)	*Desmarestia* (n = 2)	*Laminaria* (n = 14)	*Chondrus* (n = 4)	Total Occurrences as Epibiont
Phylum Arthropoda	*Balanus*	0	0	0	0	0	4	0	0	0	0	4
	Chthamalus	0	0	0	0	0	1	0	0	0	0	1
Phylum Bryozoa	*Bugula*	0	0	0	0	1	2	1	0	10	0	15
	Electra(*)	0	0	0	0	0	1	0	0	0	0	1
	Membranipora	0	0	0	0	0	0	0	0	8	2	10
	Tricellaria	0	0	0	0	0	0	0	0	1	0	1
Phylum Chlorophyta	*Ulva*(*)	0	0	0	0	3	1	0	0	0	1	5
Phylum Chordata	*Botrylloides*	1	1	0	0	0	1	1	1	6	2	13
	Ciona	0	1	1	0	0	0	0	0	2	0	4
	Didemnum	1	9	0	1	6	8	0	2	2	3	32
	Molgula	2	4	0	0	3	1	1	2	1	1	15
Phylum Cnidaria	*Obelia*(*)	0	0	0	0	0	1	0	0	0	0	1
Phylum Mollusca	*Hiatella*	0	1	0	0	0	0	0	0	0	0	1
	Macoma	0	0	0	0	0	1	0	0	0	0	1
	Mytilus	0	5	2	0	4	9	1	0	5	3	29
	Tellina	0	2	1	0	0	3	0	0	0	0	6
Phylum Ochrophyta	*Ascophyllum*	1	0	0	0	0	0	0	0	0	0	1
	Desmarestia	0	0	1	0	7	1	0	0	1	1	11
	Dictyosiphon	0	0	0	0	0	0	0	0	1	0	1
	Laminaria	0	0	0	0	1	0	0	0	0	0	1
Number epibionts		5	23	5	1	25	34	4	5	37	13	
Total taxon richness		4	7	4	1	7	13	4	3	10	5	

Each column represents a different basibiont genus, and each row represents a different epibiont genus. Gray columns and rows indicate that the genus is non-native. Boxes with bold borders show occurrences of non-native epibionts colonizing non-native epibionts. Genera marked with (*) indicate cryptogenic taxa.
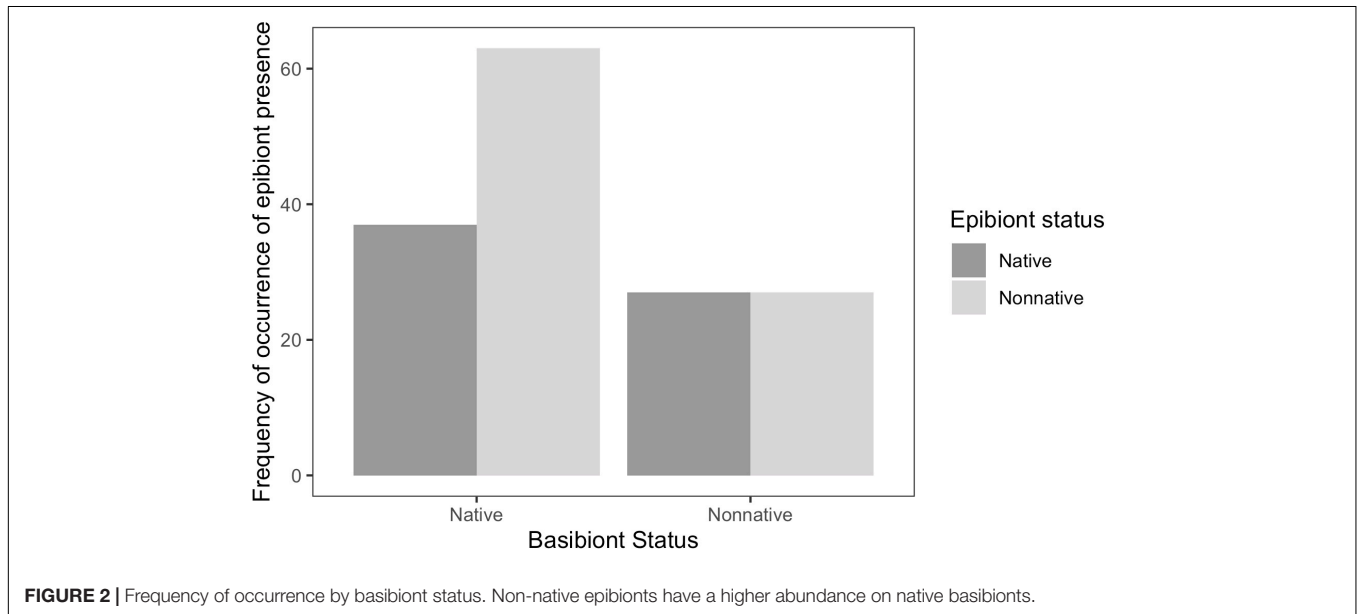
FIGURE 2 | Frequency of occurrence by basibiont status. Non-native epibionts have a higher abundance on native basibionts.

There was a significant difference in epibiont-basibiont weight ratio among basibiont phyla ($F = 3.72$; df = 4, 59; $P < 0.01$). Only Ochrophyta supported more than its own weight in epibionts (3.151 ± 0.905). The epibiont-basibiont weight ratio for Ochrophyta is significantly higher than that of Chordata (Tukey's, $P < 0.05$) and Mollusca (Tukey's, $P < 0.05$).
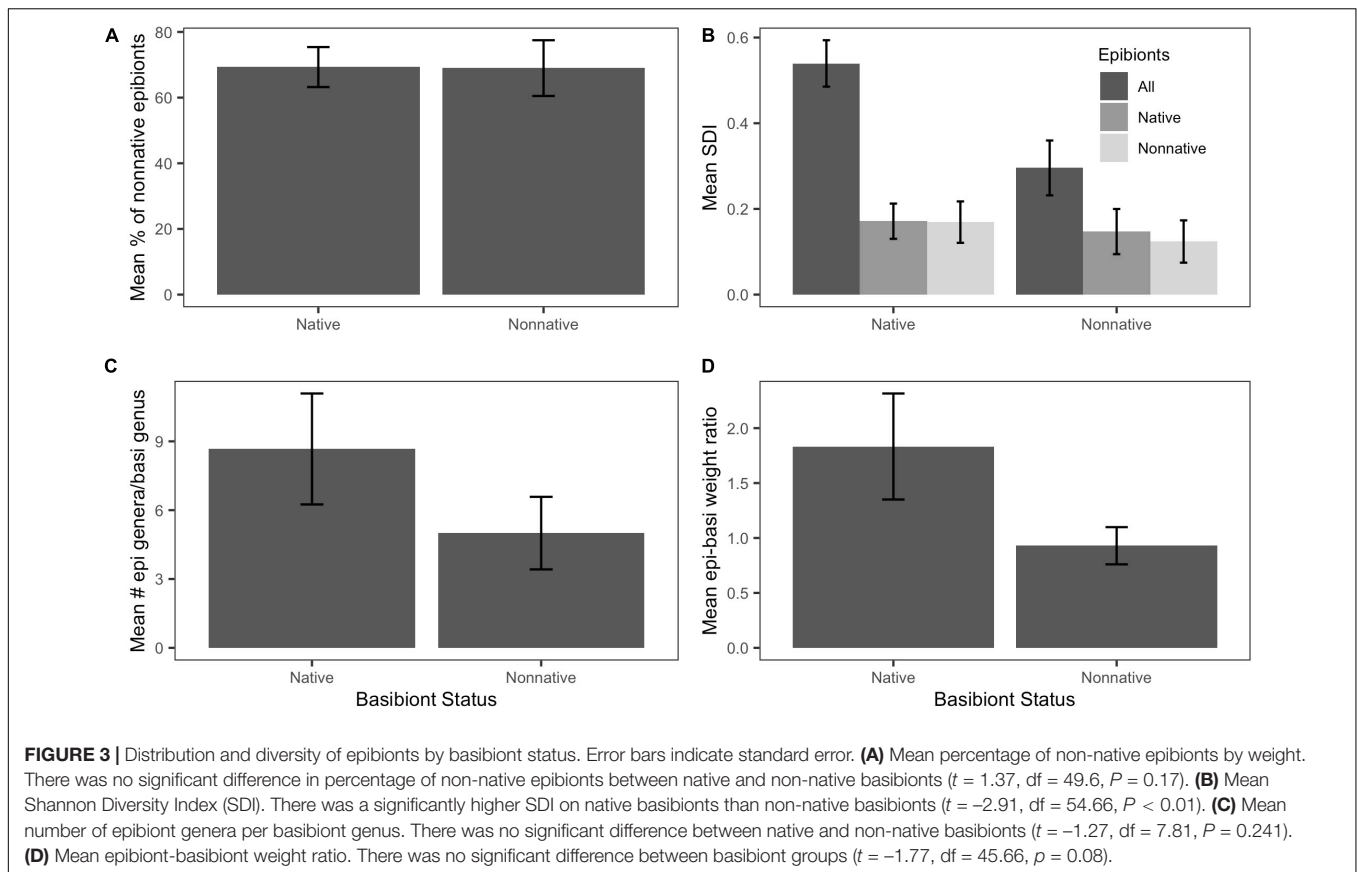
There was a significant difference in the percentage of epibionts that were non-native among basibiont phyla ($F = 0.315$; df = 4, 59; $P < 0.05$). Ochrophyta supported significantly more non-native epibionts (mostly bryozoans) than Phylum Mollusca (Tukey's, $P < 0.05$). The only non-native basibiont phylum was Chordata. Interestingly, there is a significant difference in percent epibionts that are non-native among *genera* ($F = 3.551$; df = 9, 54; $P < 0.05$), in which

Ciona harbored a higher percentage of non-native epibionts ($98.093 \pm 0.717\%$) than *Styela* ($44.905 \pm 13.677\%$), *Mytilus* ($45.910 \pm 11.416\%$), and *Laminaria* ($89.845 \pm 5.470\%$; Tukey's, $P < 0.05$).

Shannon Diversity Index varied with basibiont phyla. There was a significant difference in SDI among phyla ($F = 3.78$; df = 4, 59; $P < 0.01$). Phylum Rhodophyta (mean SDI: 0.846 ± 0.116, $n = 4$) had a significantly higher epibiont SDI than Phylum Chordata (mean SDI: 0.296 ± 0.064, $n = 26$; Tukey's, $P < 0.05$).

Does Size and Status Matter?

Due to the variation in size among the collected basibionts, we were interested in determining if size (approximated by blotted wet weight) and basibiont status were useful in predicting either

FIGURE 3 | Distribution and diversity of epibionts by basibiont status. Error bars indicate standard error. **(A)** Mean percentage of non-native epibionts by weight. There was no significant difference in percentage of non-native epibionts between native and non-native basibionts ($t = 1.37$, df $= 49.6$, $P = 0.17$). **(B)** Mean Shannon Diversity Index (SDI). There was a significantly higher SDI on native basibionts than non-native basibionts ($t = -2.91$, df $= 54.66$, $P < 0.01$). **(C)** Mean number of epibiont genera per basibiont genus. There was no significant difference between native and non-native basibionts ($t = -1.27$, df $= 7.81$, $P = 0.241$). **(D)** Mean epibiont-basibiont weight ratio. There was no significant difference between basibiont groups ($t = -1.77$, df $= 45.66$, $p = 0.08$).

percent of non-native epibionts present or total epibiont weight colonizing a basibiont. We tested the hypothesis that the effect of basibiont weight on the percentage of epibionts that are non-native depended on basibiont invasion status. We found no evidence for an interaction between basibiont weight and status on the percent of non-native epibionts ($F = 0.0285$; df $= 1, 60$; $P = 0.867$; **Figure 4**). We also tested the hypothesis that the effect of basibiont weight on total epibiont weight depended on the invasion status of the basibiont. We again found no interaction between basibiont weight and status on total epibiont weight ($F = 0.401$; df $= 1, 60$; $P = 0.529$; **Figure 5**). In both cases, the effects of basibiont and status were additive. All larger basibionts (weighing above 20 grams) were native.

DISCUSSION

In our study, there was no relationship between epibiont and basibiont status. However, while we found no preference for basibiont by status, there was a significantly more diverse assemblage of epibionts on native basibionts. This suggests that non-native basibiont species do not support as many epibiont species as native basibiont taxa.
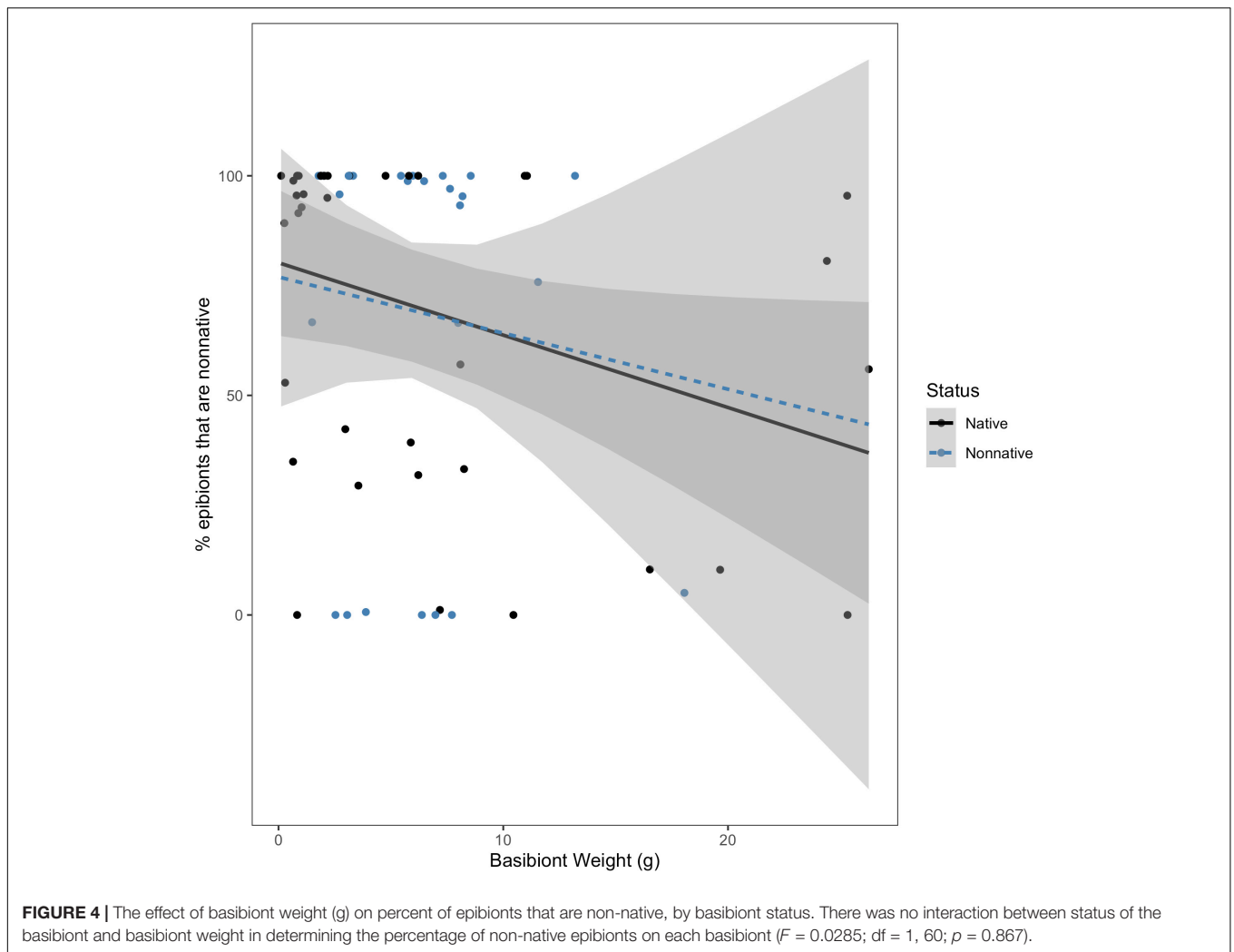
Basibiont Status
The data we gathered may suggest that non-native basibiont organisms inhabiting an area may result in lower biodiversity

of associated epibionts. There is evidence in the literature that non-native species may lead to community diversity decreases overall (Blackburn et al., 2004; Gaertner et al., 2009); though the extent of such declines was dependent on the invading species and the ecosystem in which the study was conducted (Gaertner et al., 2009). Arnold et al. (2016) found that fewer epibiotic species settled on the non-native alga *Undaria pinnatifida*, compared to native members of the same phylum (*Laminaria ochroleuca, Saccharina latissima,* and *Saccorhiza polyschides*). However, contrast these findings to Munari (2008), who found that in the Mediterranean, a non-native mussel basibiont *Musculista senhousia* ultimately led to higher biodiversity in areas that it invaded. These mussels supported over double the number of non-native epibionts, when compared to native basibionts. In these studies, as well as in the current study, the focus was primarily on the diversity of epibionts on each basibiont; however, an additional factor to consider in community structure is how foundational basibiont species may ameliorate stressful habits for mobile species (e.g., the non-native *Mytilus galloprovincialis* in South Africa, per Robinson et al., 2007).

Basibiont Taxon
This contradicting evidence from Munari (2008) may simply mean that basibiont taxon characteristics matter more than basibiont invasion status in determining which epibionts will

FIGURE 4 | The effect of basibiont weight (g) on percent of epibionts that are non-native, by basibiont status. There was no interaction between status of the basibiont and basibiont weight in determining the percentage of non-native epibionts on each basibiont (F = 0.0285; df = 1, 60; p = 0.867).
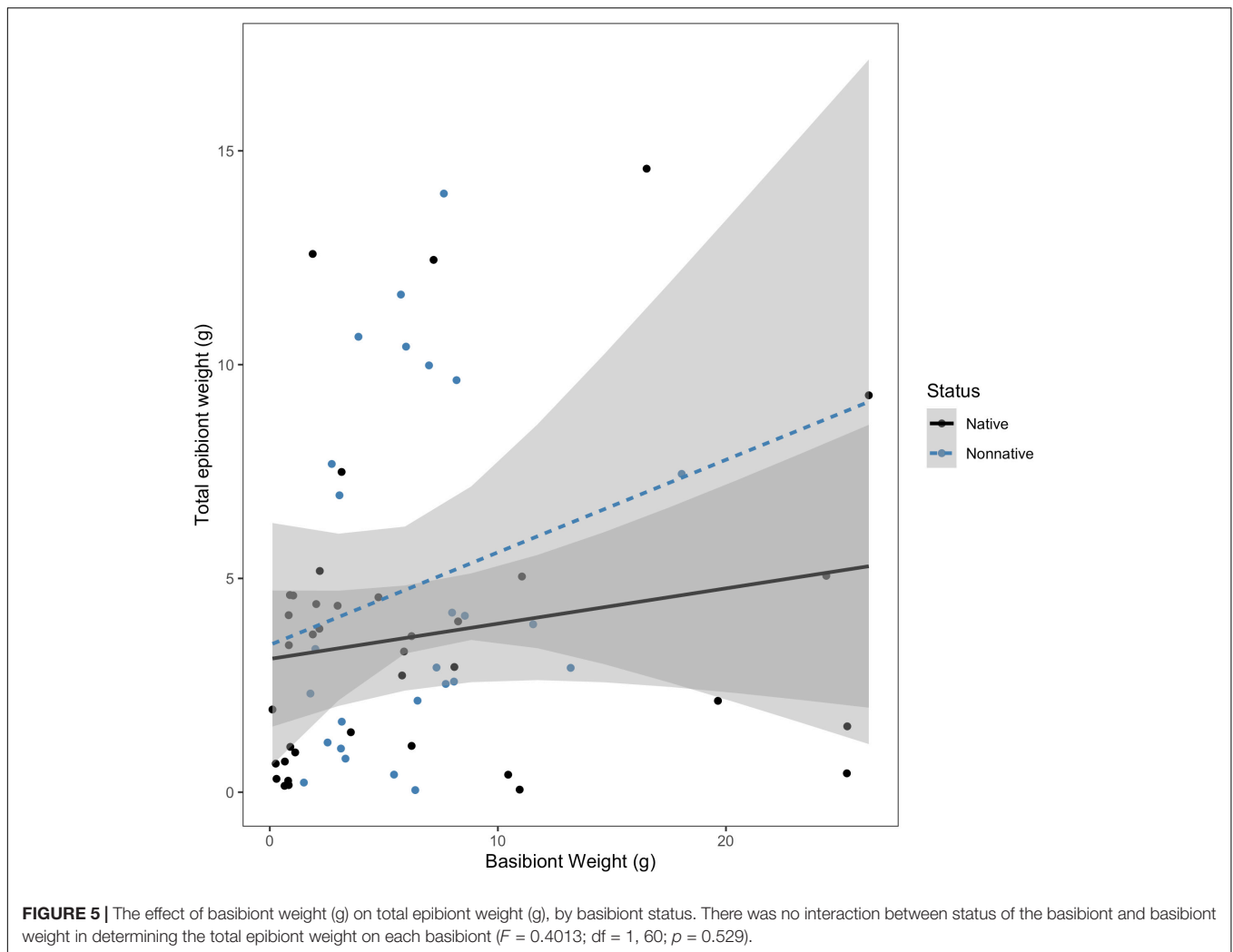
settle. In our study, mussels were the most common native basibiont taxa; therefore, mussel surface topography may be an important factor that determines settlement potential. We also found no overall relationship between basibiont status coupled with either basibiont weight (a proxy for size) on either the total weight of the epibionts on each basibiont sample or the percent of basibionts that were non-native. Instead, surface microtopography and basibiont defenses may regulate the species that settle as epibionts (Wahl, 2009). Therefore, the specific species of basibiont present in the community may determine the quality, and perhaps quantity, of settling species.

Variation of multiple surface characteristics and morphology have been shown to impact which epibionts settle on a basibiont. Basibiont microtopographies and ability to chemically control epibiosis may also determine whether epibionts will settle on a basibiont (Marszalek et al., 1979; Stachowitch, 1980; Davis et al., 1989; Wahl et al., 1998; Lee and Qian, 2003; Dobretsov et al., 2006). Defenses against epibionts vary by species (Wahl, 2009). For example, mussels possess an antifouling periostracum (Bers et al., 2006), while algal species produce secondary metabolites that prevent colonization by epibionts (Nylund et al.,

2005; Dobretsov et al., 2006). Ascidians also use mechanical and chemical defenses to minimize surface fouling (Wahl and Banaigs, 1991). Basibiont morphology also matters. Colonial animals are better competitors due to their indeterminate growth and asexual reproduction, while solitary animals survive due to their size and aggregation (e.g., mussel beds; Jackson, 1977). Drakard and Lanfranco (2016) found that macroalgal basibiont age (estimated by size) and surface area (estimated by coarseness) best predicted total abundance of epibionts, with the former measurement positively predicting species richness.

In our study, mussels supported the most epibiont phyla. Mussels, as ecosystem engineers, are a fundamental part of marine communities because they alter the substrate and facilitate interactions with many other species resulting in complex habitats (Jones et al., 1994; Gutiérrez et al., 2003; Robinson et al., 2007; Gutiérrez et al., 2019). Species richness increases in the presence of aggregating mussels (Seed, 1996; Chintiroglou et al., 2004; Borthagaray and Carranza, 2007). Mussels provide both substrate and food resources for interstitial and other associated species (Thiel and Ullrich, 2002). Çinar et al. (2008) found that *Mytilus galloprovincialis* assemblages

FIGURE 5 | The effect of basibiont weight (g) on total epibiont weight (g), by basibiont status. There was no interaction between status of the basibiont and basibiont weight in determining the total epibiont weight on each basibiont (F = 0.4013; df = 1, 60; p = 0.529).

supported non-native species, about 31% of the total individuals found in their study.

What Is the Role of Epibiosis in This Community?

Repeated invasion events, in which a non-native species facilitates additional invasions, may create a positive feedback loop (Simberloff and Von Holle, 1999). This "invasional meltdown" results in a snowball effect in which facilitation of one invader by another further exacerbates non-native species' impacts on native species (Von Holle, 2011). Our study certainly did not demonstrate invasional meltdown as described in Simberloff (2006a). In fact, few studies directly demonstrate meltdown (Simberloff, 2006a). Gurevitch (2006) posits that invasional meltdown may be relatively uncommon and difficult to demonstrate. Very few papers show examples of marine meltdown (e.g., Grosholz, 2005; Geraldi et al., 2020); the majority of claimed meltdown events are based on terrestrial or freshwater data (e.g., Ricciardi, 2001; Jackson, 2015). Furthermore, Green et al. (2011) observe that the invasional meltdown hypothesis is

controversial as few studies show positive feedback loops between invaders, in which amplified facilitative effects exist, and no studies at the time of their paper demonstrate facilitation of entry or spread of secondary invaders. Simberloff (2006a) agrees that specific evidence to show meltdown in the literature is rare.

Simberloff (2006a,b) and Gurevitch (2006) distinguish between facilitation and positive feedback. Facilitation occurs when one species aids another but does not necessarily receive a benefit in return. Positive feedbacks describe mutual facilitation, a population-level interaction where species facilitate one another. For example, an invader facilitates a species through predator deterrence while that species in turn ameliorates a harsh environment allowing the invading species to further establish. Gurevitch (2006) further claims that meltdown is an imprecise term that may refer to positive interactions, facilitative interactions, or actual meltdown, which includes feedback between invaders, amplifying their impacts, acting as an "autocatalytic" community-level process that accelerates replacement of native communities (Simberloff, 2006b; Green et al., 2011). Both Simberloff (2006b) and Gurevitch (2006) agree that studying positive feedbacks are likely to help in

understanding invasion. Where, then, does epibiosis fall on the spectrum of facilitation, positive feedback, and meltdown? Epibiosis is not necessarily a mutualism since there are more benefits for epibiont species than basibiont species (Wahl, 1989). For example, basibionts provide additional substrate, and favorable hydrodynamic positions for filter feeding epibionts. In return, some epibionts provide potential protection against predation for basibionts, while many epibionts have been shown as harmful to basibionts (due to surface damage, competition, added weight leading to reallocation of resources away from growth, etc.; Wahl, 1989). If this is the case, then epibiosis may result in facilitation of invaders, but it is unclear if it is truly a mechanism for meltdown.

However, epibiosis may provide a vehicle for *facilitation*. Grosholz (2005) describes a model in which invaders arriving early in community establishment produce a change in the system, facilitating the establishment and spread of later invaders. In the case of epibiosis, a non-native basibiont, particularly if it is a strong competitor for space, may provide additional space for other settling species. While our study showed no preferential settlement on non-native or native basibionts, the availability of novel three-dimensional surfaces is expected to support additional species settlement. Improving habitat complexity is likely to increase potential for additional species, thereby increasing species richness (Crooks, 2002). Wonham et al. (2005) describe the facilitation of other species, including invaders, by the presence of the non-native Asian hornsnail (*Batrillaria attrimentaria*) on a mudflat. Generally, a fluctuating resource supply should increase invasions (Davis et al., 2000).

Several factors may determine invasibility of a community. Sher and Hyatt (1999) propose that both invader and environmental traits are incorporated into models predicting invasibility. Stachowicz et al. (1999) studied invasibility of marine ecosystems by looking at recruitment in sessile, suspension-feeding invertebrate communities and found that less diverse communities harbored more non-native invaders. Stachowicz et al. (2002) determined that this relationship was present at multiple scales. They found that the factors that control space availability also contributed to invasion success. Levine (2000) describes species loss at small scales reducing invasion resistance (that is, making them more prone to invasion), however, at community-level scales, diverse communities may be more likely to be invaded due to additional factors such as propagule supply (Kolar and Lodge, 2001).

Future Steps and Comments on the Study

This study is intended as an initial observational snapshot of communities in geographically close sites in Maine; it is not sufficient nor intended to be representative of patterns or the full range of taxa along coastal communities in other regions. It is not appropriate to assume that the impacts of non-native basibionts would have a similar impact in all marine ecosystems, as other factors may be at play in determining community structure (i.e., propagule pressure and other biotic components, as well as abiotic components; Lodge, 1993). The impact of an invader

may very well depend on the factors leading to formation of the community in which it has invaded (Parker et al., 1999). With an observational focus, our study used basibionts that varied in size, and likely age, which may have affected the epibionts that were present. Longer-lived and larger species may be colonized by species at a different time period than younger or smaller species, which may impact epibiont communities on each basibiont.

There are multiple opportunities to expand on our study to better understand the role of epibiosis and facilitation in marine communities. This study may further be broadened to examining the impacts of within-species size variation on epibiont composition and diversity. In addition, a phenological time-series study to determine population impact of native species both before and after invasion would be ideal (Simberloff, 2006a). We do not know how the presence of basibionts changes overall community diversity because we did not measure the diversity before and after invasion. Furthermore, by expanding this study geographically, we can look at larger scale impacts on biodiversity in areas dominated by native and non-native basibiont foundational taxa. Future research should also investigate how epibiont-basibiont relationships differ by location to determine whether trends observed in this study are universal or vary with location. According to Jackson (2015), specific interactions between associated non-native species should be studied further as it is "a critical area of ecology." As epibiosis is a relationship between two different pairs of species, it is one of the relationships that requires additional attention in understanding the structure of marine communities, and this interaction provides an excellent model to understand facilitation in nearshore communities.

CONCLUSION

Our study has indicated that while there is no direct association between epibionts and basibionts by status, native basibionts support a more diverse group of organisms. Hobbs et al. (2006) asks if novel systems are on the increase and whether such ecosystems will predominate at the end of the present century. How does this change our understanding of "wild" or "natural" ecosystems? Is invasional meltdown and other specialized concepts necessary for understanding the changes ecosystems are facing, or are they simply a typical example of ecosystem dynamics? Studies on epibiosis, particularly between non-native epibionts and their host, have focused primarily on the impacts on the basibiont (e.g., Saier and Chapman, 2004; Auker, 2010; Dijkstra and Nolan, 2011), rather than facilitative, community-wide effects. This study sheds light on the connection between epibiosis, invasion, and facilitative effects, with the hope that more studies will investigate epibiosis as a facilitator of invasions.

DATA AVAILABILITY STATEMENT

The original contributions presented in this study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

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