



HAL
open science

Positive association between epiphytes and competitiveness of the brown algal genus *Lobophora* against corals

Andreas Eich, Amanda K Ford, Maggy Nugues, Ryan S Mcandrews, Christian Wild, Sebastian Ferse, Sebastian C.A. Ferse

► To cite this version:

Andreas Eich, Amanda K Ford, Maggy Nugues, Ryan S Mcandrews, Christian Wild, et al.. Positive association between epiphytes and competitiveness of the brown algal genus *Lobophora* against corals. *PeerJ*, 2019, 7, pp.e6380. 10.7717/peerj.6380 . hal-02069476

HAL Id: hal-02069476

<https://univ-perp.hal.science/hal-02069476>

Submitted on 15 Mar 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Positive association between epiphytes and competitiveness of the brown algal genus *Lobophora* against corals

Andreas Eich^{1,2}, Amanda K. Ford^{1,2,3}, Maggy M. Nugues^{4,5},
Ryan S. McAndrews^{1,2}, Christian Wild² and Sebastian C.A. Ferse^{1,2}

¹ Department of Ecology, Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany

² Department of Marine Ecology, FB2 Biology/Chemistry, University of Bremen, Bremen, Germany

³ Stockholm University, Stockholm Resilience Centre, Stockholm, Sweden

⁴ EPHE, PSL Research University, UPVD-CNRS, USR3278, CRIOBE, Perpignan, France

⁵ Labex Corail, CRIOBE, Moorea, French Polynesia

ABSTRACT

Observations of coral–algal competition can provide valuable information about the state of coral reef ecosystems. Here, we report contact rates and apparent competition states for six shallow lagoonal reefs in Fiji. A total of 81.4% of examined coral perimeters were found to be in contact with algae, with turf algae (54.7%) and macroalgae of the genus *Lobophora* (16.8%) representing the most frequently observed contacts. Turf algae competitiveness was low, with 21.8% of coral–turf contacts being won by the algae (i.e. overgrowth or bleaching of coral tissue). In contrast, *Lobophora* competitiveness against corals was high, with 62.5% of contacts being won by the alga. The presence of epiphytic algae on *Lobophora* was associated with significantly greater algal competitiveness against corals, with 75.8% and 21.1% of interactions recorded as algal wins in the presence and absence of epiphytes, respectively. Sedimentation rate, herbivorous fish biomass, and coral colony size did not have a significant effect on *Lobophora*–coral interactions. This research indicates a novel and important role of epiphytes in driving the outcome of coral–algal contacts.

Submitted 15 June 2018

Accepted 28 December 2018

Published 8 February 2019

Corresponding author

Andreas Eich, eich.andreas@web.de

Academic editor

Joseph Pawlik

Additional Information and
Declarations can be found on
page 9

DOI 10.7717/peerj.6380

© Copyright
2019 Eich et al.

Distributed under
Creative Commons CC-BY 4.0

OPEN ACCESS

Subjects Conservation Biology, Ecology, Marine Biology

Keywords *Lobophora*, Coral algae competition, Epiphytes, Allelopathy, Turf algae

INTRODUCTION

Coral reefs are rapidly degrading worldwide, with hard corals commonly being replaced by benthic algae (*Diaz-Pulido et al., 2009*). These changes are triggered by a combination of stressors, including overfishing of herbivores, excess nutrient and organic matter input, global climate change, and emergent marine diseases (*Barott et al., 2012*). To understand the mechanisms involved in these shifts, it is important to investigate interactions between corals and algae. These interactions typically involve a range of physical, microbial, and chemical mechanisms (*McCook, Jompa & Diaz-Pulido, 2001; Barott & Rohwer, 2012*). Algae can damage corals via direct physical interactions such as shading and abrasion, the exudation of allelopathic substances, and through indirect

influences such as the release of dissolved organic carbon (DOC) (Barott & Rohwer, 2012). Microorganisms within coral mucus can profit from released DOC and deplete oxygen concentrations in proximity to coral tissue, which can subsequently cause mortality and disease (Barott & Rohwer, 2012; Jorissen et al., 2016).

Furthermore, the effects of algae on corals depend on the specific coral (Rasher et al., 2011) and algal (Jompa & McCook, 2003a; Bonaldo & Hay, 2014) species present. Crustose coralline algae generally have positive effects on coral reefs, for example, through promoting coral recruitment (Ritson-Williams et al., 2009) and suppressing macroalgal recruitment (Vermeij, Dailer & Smith, 2011), whereas turf algae can negatively influence coral health through impeding coral recruitment success (Birrell, McCook & Willis, 2005) and reducing tissue thickness (Quan-Young & Espinoza-Avalos, 2006). Anthropogenic influence (Barott et al., 2012), particularly sedimentation and terrestrial run-off, can increase the frequency of coral–turf contacts and turf competitiveness (Nugues & Roberts, 2003; Gowan, Tootell & Carpenter, 2014).

Brown macroalgae within the genus *Lobophora* have been a focus of recent research because of their rapid increase on many reefs worldwide (Mumby, Foster & Fahy, 2005). This genus can flourish following disturbances such as bleaching events (Diaz-Pulido et al., 2009) and storms (Roff et al., 2015), reaching benthic cover of up to 50% (Slattery & Lesser, 2014). Direct contact between *Lobophora* and corals commonly induces coral bleaching and mortality (Jompa & McCook, 2002; Slattery & Lesser, 2014; Vieira et al., 2016a) and results in decreased coral growth, reproduction, and recruitment (Nugues & Bak, 2006). *Lobophora* can also act as a substrate for a diverse epiphytic community (Fricke et al., 2011). However, few studies to date have considered the roles of epiphytes in coral–algal interactions or have distinguished the effects of epiphytes from those of their algal hosts.

Epiphytes have a wide range of effects on their host, and consequently their influence on host competitiveness is challenging to predict. Epiphytes can stress their host through shading (Round, 1981), can reduce consumption of host algae by herbivores (D'Antonio, 1985; Fong, Smith & Wartian, 2006; Smith et al., 2010), and if firmly attached can lead to tissue lesions and/or cause bacterial infections (Fricke et al., 2013). Some epiphytes are hemiparasitic and drain organic carbon from their host using penetrating rhizoids (Garbary & Deckert, 2002). If epiphytes act as a stressor to their algal host and reduce algal growth rates, they could potentially decrease the competitiveness of their algal hosts against corals. Alternatively, epiphytes could reinforce competitiveness of their algal hosts by directly damaging corals. For example, a common epiphyte of *Lobophora*, *Anotrichum tenue* (Fricke et al., 2011), can overgrow living coral tissue (Jompa & McCook, 2003b). Furthermore, by altering the composition and concentration of secondary metabolites in their host (Kremb et al., 2014), epiphytes can deter herbivorous fishes from consuming algal hosts (Karez, Engelbert & Sommer, 2000) and thus increase host competitiveness.

The goal of this observational study was to assess the types and outcomes of coral–algal interactions on coral reefs in Fiji and to gain first insights into the relationship between the presence of epiphytes and algal host competitiveness against corals. In addition

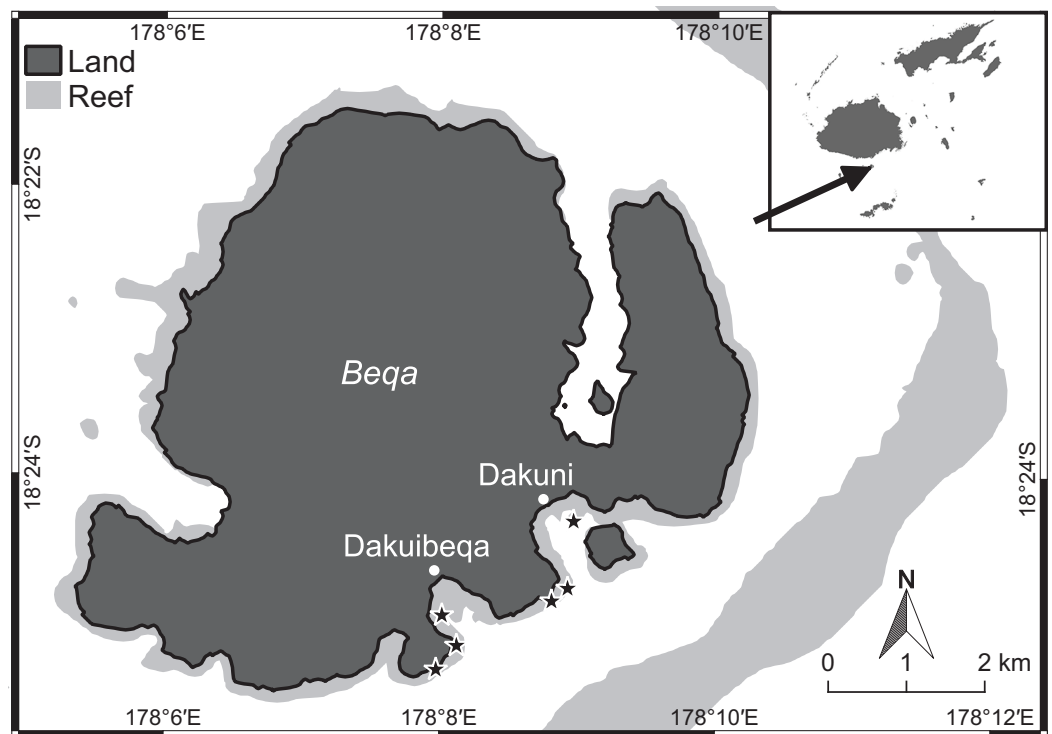


Figure 1 Beqa island in the south of Fiji (see arrow) with locations of the six study sites (stars) close to the village of Dakuibeqa and Dakuni. [Full-size](#) DOI: 10.7717/peerj.6380/fig-1

to characterising the coral–algal interactions and recording the genera involved, we measured herbivorous fish biomass and sedimentation rates as explanatory variables. We expected a negative relationship between herbivorous fish biomass and the number of coral–algal interactions, and also anticipated that higher sedimentation rates would enhance the prevalence of turf algae involved in interactions by deterring herbivory (Bellwood & Fulton, 2008).

MATERIAL AND METHODS

Benthic surveys were conducted at two sets of three shallow lagoonal reef sites (four to six m depth) with increasing distance from each of two rural villages at Beqa Island (18°25'S, 178°08'E), Fiji (Fig. 1). At each reef, three 10 m transects were haphazardly placed on the benthos. For the first 10 hard coral colonies underneath each transect, we measured (to the nearest centimetre) the coral perimeter in contact with specific organisms (e.g. algal types, sponges, other corals) and bare substrate, thus additionally obtaining the total perimeter of the coral colony. For each observed coral–algal contact, we recorded the coral and algal genera, the presence of epiphytic algae, and the apparent outcome of the interaction. In this study, epiphytes were defined as all filamentous algae growing on the surface of macroalgae (Fig. 2) and turf algae as filamentous algae with a canopy height below two cm growing on abiotic substrate. A coral–algal interaction was considered as ‘alga-winning’ if the coral was bleached below or next to the interaction zone or if there was visible overgrowth of the alga over the coral surface, as ‘coral-winning’ if the

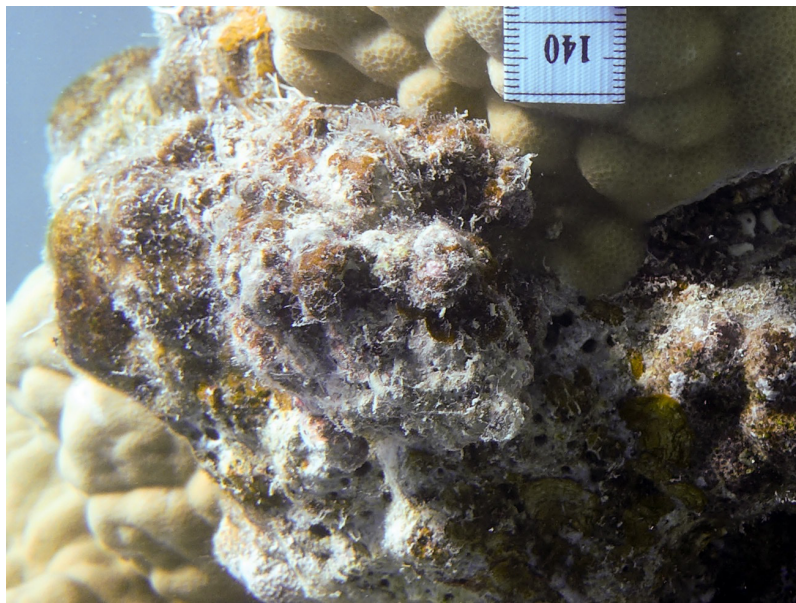


Figure 2 *Lobophora* covered with filamentous epiphytes Scale ticks are in mm. Photo by Andreas Eich.

Full-size  DOI: [10.7717/peerj.6380/fig-2](https://doi.org/10.7717/peerj.6380/fig-2)

coral was visibly overgrowing the algae, or as ‘neutral’ if neither was observed (Barott *et al.*, 2012).

At each site, three sediment traps, designed according to Storlazzi, Field & Bothner (2011), were deployed three times, each for *ca.* 3 weeks. Sediment material was filtered, dried for 24 h at 105 °C, and weighed. The abundance of herbivorous fishes (according to categorisations by Green & Bellwood, 2009) was assessed for six 30 × 5 m belt transects per site. Mobile and large fishes (>10 cm fork length) were counted in a first pass along the transect tape, and smaller, site-attached fishes were counted on the return pass. All surveys were performed by one surveyor (RSM) at approximately the same time of day (morning–noon), tide (outgoing), and weather conditions (calm) within 1 month (30.09.2015–29.10.2015). Fishes were categorised into five cm size classes (fork length) and the average fish biomass per site was calculated as described by Froese (2006), using species-specific length-weight conversion factors (Green & Bellwood, 2009).

For each coral colony, the proportion of the colony perimeter in contact with each type of contact category (i.e. algal genera, other benthic organisms, or bare substrate) was calculated (hereon referred to as ‘contact rate’). The two most frequently observed algal groups (i.e. turf and *Lobophora*) were analysed in more detail. For both types of algae, the relationship between contact rate and site was analysed with a generalised linear model. For contacts with turf algae, a generalised linear mixed model incorporating transect nested in site as a random effect was applied to analyse the relationships between contact rate and sedimentation rate, herbivorous fish biomass, coral genus, and colony size (perimeter). For contacts with *Lobophora*, we also tested the effect of the presence of epiphytes. Furthermore, models were run separately for each of the three most frequently observed coral genera. Following the same approach, the influence of the

above parameters on the competitiveness of turf algae and *Lobophora* was tested for each coral genus incorporating a random factor for the coral colony ID. Competitiveness was defined as the proportion of the coral perimeter in contact with turf algae or *Lobophora* for which the interaction was classified as ‘alga-winning’. Since response values consisted of proportions, a beta distribution was chosen for all models (Kieschnick & McCullough, 2003). Proportional data contained the extremes (0 and 1) and was therefore transformed by $(y(n-1) + 0.5)/n$, where n is the sample size (Smithson & Verkuilen, 2006). Comparisons of groups (i.e. tests comparing between different sites and presence or absence of epiphytes) were only conducted if at least two groups with at least three replicates each were present after sub-setting the dataframe for the separate analyses of coral genera. All models were reduced by removing the least significant term if a likelihood ratio test between the reduced and unreduced model revealed no significant difference. The effects of explanatory variables were tested using Wald tests. To account for multiple comparisons, p -values within individual analyses (i.e. of contact rate and competitiveness, respectively, both for turf algae and *Lobophora*) were adjusted after Holm (1979). All statistical analyses were carried out using R (Version 3.4.2).

RESULTS

On average, $81.4\% \pm 2.7\%$ (mean \pm SE, $n = 179$ colonies) of coral perimeters and 156 of the 179 colonies examined were in contact with algae. Turf algae was the most common algal group (124 affected colonies) involved in coral–algal interactions, followed by the macroalga *Lobophora* (73 affected colonies), recorded as being in contact with $54.7\% \pm 3.2\%$ and $16.8\% \pm 2.3\%$ of coral perimeters, respectively (Fig. 3). All interactions involving turf algae or *Lobophora* were classified either as ‘alga-winning’ or ‘neutral’ (i.e. no ‘coral-winning’ interactions were observed).

Contact rates with turf algae increased significantly with sedimentation, while herbivorous fish biomass, coral genus, colony size, and site had no significant effect (Table 1A). Separate analyses for the three most frequent coral genera in contact with turf algae (*Porites* $n = 67$ of 179 contacts, *Pavona* $n = 16$, and *Acropora* $n = 12$) revealed no significant effect for any of the explanatory variables and species (Table 1A). None of the explanatory variables were found to have a significant effect on turf algal competitiveness when considering all coral types ($21.8\% \pm 3.4\%$ ‘alga-winning’ contacts, Fig. 3A), or when analyses were run separately for the three most common coral genera (Table 1A). The effect of site could not be analysed for *Acropora* corals, since after sub-setting the data, only one site remained with at least three replicates. The contact rates of *Lobophora* were significantly higher when epiphytes were present (Table 1B). Sedimentation rate, herbivorous fish biomass, coral genus, site, and colony size did not influence *Lobophora* contact rate. When analysing contact rates of the three most frequent coral genera individually (*Porites* $n = 44$, *Acropora* $n = 8$, and equally frequent *Favites* and *Pavona* $n = 6$), no significant effects were found (Table 1B). Most interactions ($62.5\% \pm 5.2\%$) between *Lobophora* and corals were classified as ‘alga-winning’ (Fig. 3C), and in total $12.4\% \pm 2.1\%$ of the perimeter of all corals was negatively affected by *Lobophora* (i.e. ‘alga-winning’, Fig. 3C). Site, sedimentation rate, herbivorous fish biomass,

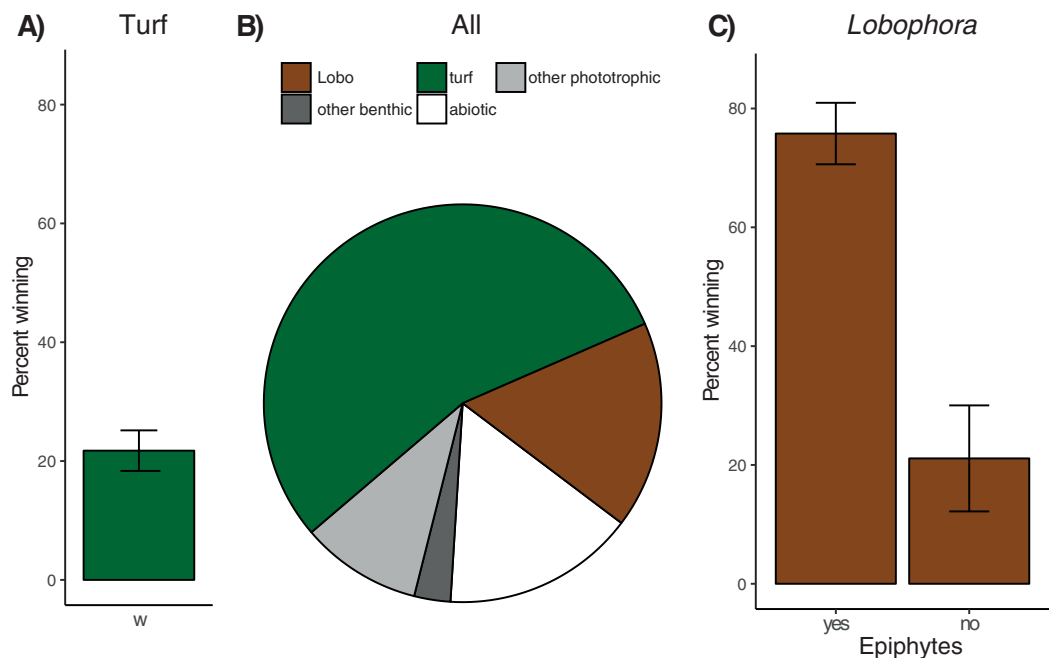


Figure 3 Overview of observed coral–algae contacts. (A) Mean percentage (\pm SE) of coral perimeter in contact with turf algae for which turf algae apparently won the interaction. (B) Proportions of coral perimeter in contact with different algae: Turf algae ('turf', green), *Lobophora* ('Lobo', brown), other phototrophic organisms like macroalgae (e.g. *Padina* or *Halimeda*) or benthic cyanobacteria ('other phototrophic', light grey), benthic invertebrates like sponges or corals ('other benthic', dark grey), and abiotic substrate like sand, rubble, or recently dead coral skeleton ('abiotic', white), (C) Mean percentage (\pm SE) of coral perimeter in contact with *Lobophora* with ('yes') and without epiphytes ('no') for which *Lobophora* apparently won the interaction. [Full-size](#) DOI: 10.7717/peerj.6380/fig-3

coral genus and colony size (perimeter) did not significantly influence *Lobophora* competitiveness. However, the presence of epiphytes had a highly significant (positive) effect on the proportion of 'alga-winning' *Lobophora*–coral interactions (Fig. 3C; Table 1B). Consistent with the results of the overall model, the presence of epiphytes increased 'alga-winning' rates for *Porites*–*Lobophora* contacts. No significant effects of the explanatory variables were found for the other coral genera (Table 1B). For *Acropora* and *Pavona*, the effects of epiphytes and site could not be analysed due to insufficient replication after sub-setting of the data. Likewise, the effect of site could not be tested for *Pavona* corals.

DISCUSSION

This study investigated the contact rates and apparent outcomes of interactions between corals and algae in a lagoonal reef system in Fiji. Contrary to our expectations, herbivorous fish biomass had no influence on coral–algal interactions. However, as expected, we found a positive correlation between the rates of sedimentation and of coral–turf algae contact. This observation was also made previously in Saint-Lucia, Caribbean (Nugues & Roberts, 2003), and in Moorea, French Polynesia (Gowan, Tootell & Carpenter, 2014), and could be explained by deterred grazing, which was not measured directly and does not necessarily have to be reflected in herbivorous fish biomass. This influence was not

Table 1 Effects of sedimentation (SED), herbivorous fish biomass (HFB), coral perimeter (CP), presence of epiphytes (EPI), site, and genus (GEN) on interactions of coral colonies with turf (A) and *Lobophora* (B).

(A) Turf

	<i>n</i>	Main effect					
		SED	HFB	CP	EPI	SITE	GEN
Contact rates							
Overall	124	$\chi^2 (df = 1) = 9.948,$ $p < 0.05$	n.s.	n.s.	–	n.s.	n.s.
Coral genus							
<i>Porites</i>	67	n.s.	n.s.	n.s.	–	n.s.	–
<i>Pavona</i>	16	n.s.	n.s.	n.s.	–	n.s.	–
<i>Acropora</i>	12	n.s.	n.s.	n.s.	–	n.s.	–
Competitiveness							
Overall	124	n.s.	n.s.	n.s.	–	n.s.	n.s.
Coral genus							
<i>Porites</i>	67	n.s.	n.s.	n.s.	–	n.s.	–
<i>Pavona</i>	16	n.s.	n.s.	n.s.	–	n.s.	–
<i>Acropora</i>	12	n.s.	n.s.	n.s.	–	n.t.	–

(B) *Lobophora*

	<i>n</i>	Main effect					
		SED	HFB	CP	EPI	SITE	GEN
Contact rates							
Overall	73	n.s.	n.s.	n.s.	$\chi^2 (df = 1) = 8.399,$ $p < 0.05$	n.s.	n.s.
Coral genus							
<i>Porites</i>	44	n.s.	n.s.	n.s.	n.s.	n.s.	–
<i>Acropora</i>	8	n.s.	n.s.	n.s.	n.s.	n.s.	–
<i>Favites</i>	6	n.s.	n.s.	n.s.	n.s.	n.s.	–
<i>Pavona</i>	6	n.s.	n.s.	n.s.	n.s.	n.s.	–
Competitiveness							
Overall	73	n.s.	n.s.	n.s.	$\chi^2 (df = 1) = 16.024,$ $p < 0.005$	n.s.	n.s.
Coral genus							
<i>Porites</i>	44	n.s.	n.s.	n.s.	$\chi^2 (df = 1) = 13.770,$ $p < 0.0005$	n.s.	–
<i>Acropora</i>	8	n.s.	n.s.	n.s.	n.t.	n.t.	–
<i>Favites</i>	6	n.s.	n.s.	n.s.	n.s.	n.t.	–
<i>Pavona</i>	6	n.s.	n.s.	n.s.	n.t.	n.t.	–

Notes:

Separate analyses were run for total percentage of contact ('contact rates', above) and for percentage of contact for which the interaction was apparently won by the alga ('competitiveness', below). Results are shown for GLM analyses of overall coral contacts with turf and *Lobophora*, and for GLMM analyses run separately for the 3 and 4 main coral genera in contact with algae, respectively. *p*-Values were adjusted for multiple comparisons after [Holm \(1979\)](#). n.s., not significant; n.t., not tested because number of groups <2 or number of replicates within groups <3.

observed when coral genera were analysed separately, probably because replication was reduced due to sub-setting of the data.

We found a negative influence of *Lobophora* on the coral perimeter, which was approximately twice as high as previously reported for *Lobophora variegata* in the Caribbean island of Curaçao ($12.4\% \pm 2.1\%$ vs. maximally 5.7% of negatively influenced coral perimeter, [Nugues & Bak, 2006](#)). Epiphytes significantly increased the proportion of interactions in which *Lobophora* were reported to be winning. We assume that this overall effect on the investigated corals was mainly caused by the high proportion of *Porites*–*Lobophora* contacts, which were strongly affected by the presence of epiphytes. Other coral genera (*Acropora*, *Favites*, and *Pavona*) were far less common, which resulted in low replication and high variance when running the model separately for these genera. The number of *Pavona* corals observed was so low that solely interactions with *Lobophora* overgrown by epiphytes were found (i.e. no interactions were recorded between *Pavona* and *Lobophora* without epiphytes present), precluding statistical analysis of this factor. Generally, results for these less common genera should be interpreted with caution.

The enhanced competitiveness when epiphytes were present on *Lobophora* could be driven by direct impacts of the epiphytes themselves on neighbouring corals and/or via indirect effects on the algal host. In New Caledonia, bleaching of coral perimeters in contact with *L. herderacea* has been proposed to be caused by associated epiphytic filamentous algae ([Vieira, Payri & De Clerck, 2015](#)). Functionally, epiphytes are similar to turf algae, which can damage corals ([McCook, Jompa & Diaz-Pulido, 2001](#); [Quan-Young & Espinoza-Avalos, 2006](#)). In this study, however, turf algae were associated with a relatively higher proportion of neutral interactions, suggesting that epiphytic filamentous algae and filamentous turf algae growing on abiotic substrate differ in their competitiveness, potentially due to differences in their species composition.

Indirect effects of epiphytic algae on coral–algal interactions could occur via chemical alterations of the algal host. For example, extracts of *Lobophora* overgrown by epiphytes have a higher activity against human immunodeficiency virus than extracts from *Lobophora* without epiphytes ([Kremb et al., 2014](#)). As *Lobophora* can damage corals via different allelochemicals ([Rasher & Hay, 2010](#); [Rasher et al., 2011](#); [Slattery & Lesser, 2014](#); [Vieira et al., 2016b](#)), increased production or concentration of any of these chemicals in the presence of epiphytes could significantly influence host competitiveness in coral–algal interactions. Another potential explanation for the elevated competitive potential of *Lobophora* with epiphytes is that epiphytes deter grazing on algal hosts ([D’Antonio, 1985](#); [Fong, Smith & Wartian, 2006](#); [Smith et al., 2010](#)). Competition with corals can induce increased algal production of allelopathic chemicals at the expense of the production of anti-herbivore substances, which can result in higher algal palatability ([Rasher & Hay, 2014](#)). If epiphytes release *Lobophora* from grazing pressure, they could further facilitate production of allelochemicals that enhance algal competitiveness without the usual associated trade-off of increased palatability. Other parameters such as the duration of the coral–*Lobophora* contact or the species composition of the epiphytal community may also have had an influence on the outcome of the competitions.

Due to infrastructure limitations stemming from a different initial scope of the study and the difficulty of accurately identifying filamentous algal species in the field, it was not possible to determine the species of epiphytes and turf algae involved in the interactions or perform an analysis of algal extracts for potential allelochemical compounds.

This constitutes an important avenue for future studies of the role of epiphytes in affecting coral–algal interactions and the underlying mechanisms.

CONCLUSIONS

These results provide strong indications that the competitiveness of *Lobophora* against corals, particularly those within the genus *Porites*, is enhanced when epiphytes are growing on *Lobophora*. This study suggests a need to consider associated epiphytic algal communities when investigating coral–algal interactions. Although this study was limited in its scope and was unable to characterise the epiphytic assemblage or the chemical compounds involved in the *Lobophora*–coral contacts, we hope that future studies will extend on our findings to better understand the dynamics of coral–algal interactions. Further research could additionally experimentally manipulate epiphytes to determine whether this observation is a result of direct negative effects of epiphytic algae on corals or of an increased competitiveness of *Lobophora* and should investigate potential differences in algal communities growing on dead corals vs. on macroalgae.

ACKNOWLEDGEMENTS

We would like to thank the village elders of Dakuibeqa for research permission, and Manassa and Bose for their help during fieldwork. Furthermore, we want to thank the ZMT dive team for their support. Comments by two anonymous reviewers helped to improve the manuscript. The research reported in this paper contributes to the Programme on Ecosystem Change and Society (www.pecs-science.org).

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This work was supported by the (German) Federal Ministry of Education and Research (BMBF) through the ‘Nachwuchsgruppen Globaler Wandel 4 + 1’ (REPICORE, grant number 01LN1303A). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
(German) Federal Ministry of Education and Research (BMBF) through the ‘Nachwuchsgruppen Globaler Wandel 4 + 1’ (REPICORE): 01LN1303A.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Andreas Eich conceived and designed the experiments, performed the experiments, analysed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Amanda K. Ford conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, approved the final draft.
- Maggy M. Nagues conceived and designed the experiments, authored or reviewed drafts of the paper, approved the final draft.
- Ryan S. McAndrews performed the experiments, authored or reviewed drafts of the paper, approved the final draft.
- Christian Wild conceived and designed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.
- Sebastian C.A. Ferse conceived and designed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

Data Availability

The following information was supplied regarding data availability:

All raw data are available in [Supplemental Files](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.6380#supplemental-information>.

REFERENCES

- Barott KL, Rohwer FL. 2012.** Unseen players shape benthic competition on coral reefs. *Trends in Microbiology* **20**(12):621–628 DOI [10.1016/j.tim.2012.08.004](https://doi.org/10.1016/j.tim.2012.08.004).
- Barott KL, Williams GJ, Vermeij MJA, Harris J, Smith JE, Rohwer FL, Sandin SA. 2012.** Natural history of coral-algae competition across a gradient of human activity in the Line Islands. *Marine Ecology Progress Series* **460**:1–12 DOI [10.3354/meps09874](https://doi.org/10.3354/meps09874).
- Bellwood DR, Fulton CJ. 2008.** Sediment-mediated suppression of herbivory on coral reefs: decreasing resilience to rising sea-levels and climate change? *Limnology and Oceanography* **53**(6):2695–2701 DOI [10.4319/lo.2008.53.6.2695](https://doi.org/10.4319/lo.2008.53.6.2695).
- Birrell CL, McCook LJ, Willis BL. 2005.** Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin* **51**(1–4):408–414 DOI [10.1016/j.marpolbul.2004.10.022](https://doi.org/10.1016/j.marpolbul.2004.10.022).
- Bonaldo RM, Hay ME. 2014.** Seaweed-coral interactions: variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. *PLOS ONE* **9**(1):e85786 DOI [10.1371/journal.pone.0085786](https://doi.org/10.1371/journal.pone.0085786).
- D'Antonio C. 1985.** Epiphytes on the rocky intertidal red alga *Rhodomela larix* (Turner) C. Agardh: negative effects on the host and food for herbivores? *Journal of Experimental Marine Biology and Ecology* **86**(3):197–218 DOI [10.1016/0022-0981\(85\)90103-0](https://doi.org/10.1016/0022-0981(85)90103-0).
- Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R, Roff G, Kline DI, Weeks S, Evans RD, Williamson DH, Hoegh-Guldberg O. 2009.** Doom and boom on a resilient reef: climate

- change, algal overgrowth and coral recovery. *PLOS ONE* **4**(4):e5239
DOI [10.1371/journal.pone.0005239](https://doi.org/10.1371/journal.pone.0005239).
- Fricke A, Titlyanova TV, Nugues MM, Bischof K. 2011.** Depth-related variation in epiphytic communities growing on the brown alga *Lobophora variegata* in a Caribbean coral reef. *Coral Reefs* **30**(4):967–973 DOI [10.1007/s00338-011-0772-0](https://doi.org/10.1007/s00338-011-0772-0).
- Fricke A, Titlyanova TV, Nugues MM, Bischof K. 2013.** *Neosiphonia howei* (Ceramiales: Rhodomelaceae)—a common epiphyte of the spreading coral reef alga *Lobophora variegata* (Dictyotales: Dictyotaceae). *Marine Biodiversity Records* **6**:1–6.
- Froese R. 2006.** Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* **22**(4):241–253
DOI [10.1111/j.1439-0426.2006.00805.x](https://doi.org/10.1111/j.1439-0426.2006.00805.x).
- Fong P, Smith TB, Wartian MJ. 2006.** Epiphytic cyanobacteria maintain shifts to macroalgal dominance on coral reefs following ENSO disturbance. *Ecology* **87**(5):1162–1168
DOI [10.1890/0012-9658\(2006\)87\[1162:ecmstm\]2.0.co;2](https://doi.org/10.1890/0012-9658(2006)87[1162:ecmstm]2.0.co;2).
- Garbary DJ, Deckert RJ. 2002.** Three part harmony—ascophyllum and its symbionts. In: Seckbach J, ed. *Symbiosis: Mechanisms and Model Systems*. Dordrecht: Springer Netherlands, 309–321.
- Green AL, Bellwood DR. 2009.** *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience—A practical guide for coral reef managers in the Asia Pacific region*. Switzerland: IUCN Work Gr Clim Chang Coral Reefs.
- Gowan JC, Tootell JS, Carpenter RC. 2014.** The effects of water flow and sedimentation on interactions between massive *Porites* and algal turf. *Coral Reefs* **33**(3):651–663
DOI [10.1007/s00338-014-1154-1](https://doi.org/10.1007/s00338-014-1154-1).
- Holm S. 1979.** A simple sequentially rejective multiple test procedure a simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* **6**:65–70.
- Jompa J, McCook LJ. 2002.** The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). *Limnology and Oceanography* **47**(2):527–534 DOI [10.4319/lo.2002.47.2.0527](https://doi.org/10.4319/lo.2002.47.2.0527).
- Jompa J, McCook LJ. 2003a.** Coral-algal competition: macroalgae with different properties have different effects on corals. *Marine Ecology Progress Series* **258**:87–95
DOI [10.3354/meps258087](https://doi.org/10.3354/meps258087).
- Jompa J, McCook LJ. 2003b.** Contrasting effects of turf algae on corals: massive *Porites* spp. are unaffected by mixed-species turfs, but killed by the red alga *Anotrichium tenue*. *Marine Ecology Progress Series* **258**:79–86 DOI [10.3354/meps258079](https://doi.org/10.3354/meps258079).
- Jorissen H, Skinner C, Osinga R, De Beer D, Nugues MM. 2016.** Evidence for water-mediated mechanisms in coral–algal interactions. *Proceedings of the Royal Society B: Biological Sciences* **283**(1836):20161137 DOI [10.1098/rspb.2016.1137](https://doi.org/10.1098/rspb.2016.1137).
- Karez R, Engelbert S, Sommer U. 2000.** “Co-consumption” and “protective coating”: two new proposed effects of epiphytes on their macroalgal hosts in mesograzer-epiphyte-host interactions. *Marine Ecology Progress Series* **205**:85–93 DOI [10.3354/meps205085](https://doi.org/10.3354/meps205085).
- Kieschnick R, McCullough BD. 2003.** Regression analysis of variates observed on (0, 1): percentages, proportions and fractions. *Statistical Modelling: An International Journal* **3**(3):193–213 DOI [10.1191/1471082x03st053oa](https://doi.org/10.1191/1471082x03st053oa).
- Kremb S, Helfer M, Kraus B, Wolff H, Wild C, Schneider M, Voolstra CR, Brack-Werner R. 2014.** Aqueous extracts of the marine brown alga *Lobophora variegata* inhibit HIV-1 infection at the level of virus entry into cells. *PLOS ONE* **9**(8):e103895
DOI [10.1371/journal.pone.0103895](https://doi.org/10.1371/journal.pone.0103895).

- McCook LJ, Jompa J, Diaz-Pulido G. 2001.** Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs* **19**(4):400–417 DOI [10.1007/s00338000129](https://doi.org/10.1007/s00338000129).
- Mumby PJ, Foster NL, Fahy EAG. 2005.** Patch dynamics of coral reef macroalgae under chronic and acute disturbance. *Coral Reefs* **24**(4):681–692 DOI [10.1007/s00338-005-0058-5](https://doi.org/10.1007/s00338-005-0058-5).
- Nugues MM, Bak RPM. 2006.** Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. *Marine Ecology Progress Series* **315**:75–86 DOI [10.3354/meps315075](https://doi.org/10.3354/meps315075).
- Nugues MM, Roberts CM. 2003.** Coral mortality and interaction with algae in relation to sedimentation. *Coral Reefs* **22**(4):507–516 DOI [10.1007/s00338-003-0338-x](https://doi.org/10.1007/s00338-003-0338-x).
- Quan-Young LI, Espinoza-Avalos J. 2006.** Reduction of zooxanthellae density, chlorophyll a concentration, and tissue thickness of the coral *Montastraea faveolata* (Scleractinia) when competing with mixed turf algae. *Limnology and Oceanography* **51**(2):1159–1166 DOI [10.4319/lo.2006.51.2.1159](https://doi.org/10.4319/lo.2006.51.2.1159).
- Rasher DB, Hay ME. 2010.** Chemically rich seaweeds poison corals when not controlled by herbivores. *Proceedings of the National Academy of Sciences of the United States of America* **107**(21):9683–9688 DOI [10.1073/pnas.0912095107](https://doi.org/10.1073/pnas.0912095107).
- Rasher DB, Hay ME. 2014.** Competition induces allelopathy but suppresses growth and anti-herbivore defence in a chemically rich seaweed. *Proceedings of the Royal Society B: Biological Sciences* **281**(1777):20132615 DOI [10.1098/rspb.2013.2615](https://doi.org/10.1098/rspb.2013.2615).
- Rasher DB, Stout EP, Engel S, Kubanek J, Hay ME. 2011.** Macroalgal terpenes function as allelopathic agents against reef corals. *Proceedings of the National Academy of Sciences of the United States of America* **108**(43):17726–17731 DOI [10.1073/pnas.1108628108](https://doi.org/10.1073/pnas.1108628108).
- Ritson-Williams R, Arnold SN, Fogarty ND, Steneck RS, Vermeij MJA, Paul VJ. 2009.** New perspectives on ecological mechanisms affecting coral recruitment on reefs. *Smithsonian Contributions to the Marine Sciences* **38**:437–457 DOI [10.5479/si.01960768.38.437](https://doi.org/10.5479/si.01960768.38.437).
- Roff G, Doropoulos C, Zupan M, Rogers A, Steneck RS, Golbuu Y, Mumby PJ. 2015.** Phase shift facilitation following cyclone disturbance on coral reefs. *Oecologia* **178**(4):1193–1203 DOI [10.1007/s00442-015-3282-x](https://doi.org/10.1007/s00442-015-3282-x).
- Round FE. 1981.** *The ecology of algae*. Cambridge: Cambridge University Press.
- Slattery M, Lesser MP. 2014.** Allelopathy in the tropical alga *Lobophora variegata* (Phaeophyceae): mechanistic basis for a phase shift on mesophotic coral reefs? *Journal of Phycology* **50**(3):493–505 DOI [10.1111/jpy.12160](https://doi.org/10.1111/jpy.12160).
- Smith TB, Fong P, Kennison R, Smith J. 2010.** Spatial refuges and associational defenses promote harmful blooms of the alga *Caulerpa sertularioides* onto coral reefs. *Oecologia* **164**(4):1039–1048 DOI [10.1007/s00442-010-1698-x](https://doi.org/10.1007/s00442-010-1698-x).
- Smithson M, Verkuilen J. 2006.** A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods* **11**(1):54–71 DOI [10.1037/1082-989x.11.1.54](https://doi.org/10.1037/1082-989x.11.1.54).
- Storlazzi CD, Field ME, Bothner MH. 2011.** The use (and misuse) of sediment traps in coral reef environments: theory, observations, and suggested protocols. *Coral Reefs* **30**(1):23–38 DOI [10.1007/s00338-010-0705-3](https://doi.org/10.1007/s00338-010-0705-3).
- Vermeij MJA, Dailer ML, Smith CM. 2011.** Crustose coralline algae can suppress macroalgal growth and recruitment on Hawaiian coral reefs. *Marine Ecology Progress Series* **422**:1–7 DOI [10.3354/meps08964](https://doi.org/10.3354/meps08964).

- Vieira C, Engelen AH, Guentas L, Aires T, Houlbreque F, Gaubert J, Serrao EA, De Clerck O, Payri CE. 2016a.** Species specificity of bacteria associated to the brown seaweeds *Lobophora* (Dictyotales, Phaeophyceae) and their potential for induction of rapid coral bleaching in *Acropora muricata*. *Frontiers in Microbiology* 7:1–13.
- Vieira C, Payri C, De Clerck O. 2015.** Overgrowth and killing of corals by the brown alga *Lobophora hederacea* (Dictyotales, Phaeophyceae) on healthy reefs in New Caledonia: a new case of the epizoism syndrome. *Phycological Research* 63(2):152–153
[DOI 10.1111/pre.12082](https://doi.org/10.1111/pre.12082).
- Vieira C, Thomas OP, Culioli G, Genta-Jouve G, Houlbreque F, Gaubert J, De Clerck O, Payri CE. 2016b.** Allelopathic interactions between the brown algal genus *Lobophora* (Dictyotales, Phaeophyceae) and scleractinian corals. *Scientific Reports* 6(1):18637
[DOI 10.1038/srep18637](https://doi.org/10.1038/srep18637).