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Contact-free impacts of sessile reef organisms on stony coral productivity

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Coral reefs are biodiversity and productivity hotspots where space limitation makes interactions between organisms inevitable. Biodiversity loss alters these interactions, however downstream effects on the productivity of individual species remain unexplored. Here, we quantified immediate and long-term changes in stony coral productivity in response to contact-free interactions with various benthic organisms (stony corals, soft corals, macroalgae, sponges). We show that corals sense the presence of other organisms and subsequently modulate their productivity. Each stony coral species had a characteristic reaction to contact-free stimuli, while the identity of the interaction partner was of subordinate importance. Our data highlight downstream effects that biodiversity loss and shifting coral reef communities may have through indirect modulation of productivity, resulting in uneven effects among species. The productivity response is probably mediated by secondary metabolites released into the water. The underlying communication pathways that mediate these interactions remain to be investigated.

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The influence of biodiversity on ecosystem productivity can be greater than that of climate or nutrient availability[1]. High biodiversity promotes stability against disturbance[2], so that diversity loss causes further vulnerability of the ecosystem and its functions. Climate change leads to a rapid loss of biodiversity[3], with severe impacts on ecosystem services[4]. Coral reefs are the marine ecosystem with the highest biodiversity, which is why they are productivity hotspots of ecological and economic importance[5]. These ecosystems in particular are affected by climate change, and half of the coral reefs globally have already been decimated by marine heat waves[6,7].

Space in the coral reef is severely limited, making interactions between the growing organisms inevitable[8]. These can be classified as interactions, in which organisms come into physical contact, further referred to as contact-based interactions, or contact-free interactions, in which an effect is mediated without physical touch[8]. Contact-based interactions between corals and other organisms include aggressive defense mechanisms such as the extension of mesenterial filaments and sweeper tentacles[9,10], or overgrowth of other colonies[11]. Contact-free interactions include shading[12] and biocommunication[13], which is the release of secondary metabolites by organisms into the water[13,14] that in turn affect other organisms[15,16].

Interactions between species may affect their productivity, with contact-based interactions often impairing coral health and productivity[17,18]. For instance, intraspecific interactions between *Acropora hemprichii* (Ehrenberg 1834) colonies caused tissue discoloration, which indicates immune activity and overgrowth of neighboring colonies[19]. Other studies demonstrated similar negative effects after contact with various macroalgae or zoanthids, which caused tissue hypoxia[20], damage, and color change[21] in the stony coral *Orbicella annularis* (Ellis & Solander 1786)[20] or the hydrocoral *Millepora alcicornis* (Esper 1790)[21]. Contact-based interactions between stony corals also reduced growth rates[10], probably because of the energetic expenses of direct competition[10,22,23].

In contrast, an increase in productivity was reported for most contact-free interactions between stony coral species[8,18,24]. For example, the growth rate or mass change of stony corals was increased in multispecies assemblages in comparison to single-species assemblages[8,24]. Remarkably, the increase in mass in multispecies assemblages was even higher than that of the strongest single species of the study[24]. A similar effect could be observed with regard to primary production. In the study by McWilliam et al. 2018[18], increased net photosynthesis in multispecies assemblages compared to single species was described under high flow. Exceptions to these positive biodiversity effects include reduced calcification due to ocean acidification that could be neutralized in conspecific species assemblages but not in multispecies assemblages[25]. Overall, these data show the potential of contact-free interactions to boost productivity in coral reefs, even though complex patterns with environmental conditions may exist.

Confounding parameters such as complex community structures as well as environmental variability of coral reefs hamper the quantification of productivity effects between single- or mixed-species assemblages[26]. In settings with high biodiversity, a high number of potential interactions between species may arise that need to be deconstructed. Hence, analyses of individual species without confounding variables and their responses to contact-free stimulation by different sessile organisms are necessary to understand productivity changes and how they are related to shifts in coral reef communities.

To systematically quantify the effects of contact-free interactions with other sessile organisms on coral productivity, we conducted two laboratory experiments. In the first experiment, we measured the immediate effect of experimental exposure to contact-free stimuli on the photosynthetic rate of three coral species. In the second experiment, we measured the productivity of five coral species exposed to different biodiversity settings in the long-term. We hypothesized, that the productivity of stony corals changes immediately in contact-free interactions with other sessile reef organisms, depending on the interaction partner and that biodiversity has a species-specific influence on the productivity of stony corals in the long-term.

Our data highlight potential downstream effects of biodiversity loss on community composition in reef ecosystems through indirect modulation of productivity of each individual organism and species. Knowing the effects of such interactions on productivity can considerably improve restoration projects, by combining species that boost each other's productivity. Understanding the diverse interactions between the different coral reef organisms will also help us comprehend the trajectories of coral reef communities under rapid environmental changes[27].

Results

Our experiments tested the effects of contact-free stimulation by different functional groups of reef organisms on the productivity of stony corals. Both immediate (Experiment 1) and long-term (Experiment 2) effects were detected.

Immediate effects of contact-free stimuli on stony-coral productivity (Experiment 1). We detected an immediate effect of contact-free stimuli on the productivity of stony corals. Interestingly, the direction of the effect was dependent on the incubated coral species rather than on the conditioning organism providing the stimulus. *P. rus* exposed to heterospecific stimuli generally decreased productivity compared to the self-conditioned control (Fig. 1, Supplementary Table 3), *P. verrucosa* generally increased productivity (Fig. 1, Supplementary Table 3), and productivity of *S. pistillata* remained similar between heterospecific stimuli and control treatment (Fig. 1, Supplementary Table 3).

In addition to the main effects in the productivity response between incubated coral species to heterospecific stimuli, we observed specific effects of each conditioning organism (Fig. 2). Each conditioning organism elicited decreased productivity in *P. rus* compared to the self-conditioned control (−11.6- −18%) and the difference in effect size between the conditioning organisms was small (Fig. 2a-c). *Caulerpa* sp. and *H. cnidata* had the most positive effect on the photosynthetic rate in *P. verrucosa*. (34.8-41.2 %), while productivity was lowest when conditioned with *A. muricata*, which was in a range with the productivity of the self-conditioned control (Fig. 2d-f, Supplementary Table 4). *Stylophora pistillata* remained largely unaffected by all heterospecific stimuli; only the two soft corals significantly decreased its photosynthetic rate (Fig. 2g-i, Supplementary Table 4).

We ranked the mean values of each conditioning organism per incubated species and parameter from the most negative effects on coral productivity (low ranks) to most positive effects (high ranks) (Fig. 3). These analyses highlighted a similar pattern in the effect of the conditioning organisms on net and gross photosynthesis, with minor changes in ranking between incubated species (Fig. 3a, c). The stimuli by the two conditioning stony coral species consistently elicited the most negative effects on the productivity of all incubated species. Stimulation by *A. muricata* resulted in the overall lowest productivity in *P. rus* and even in *P. verrucosa*, which otherwise increased productivity in response to heterospecific stimuli. The sponge *H. cnidata* had the most positive effect on the productivity of all coral species (Fig. 3). Respiration was affected differently than photosynthesis

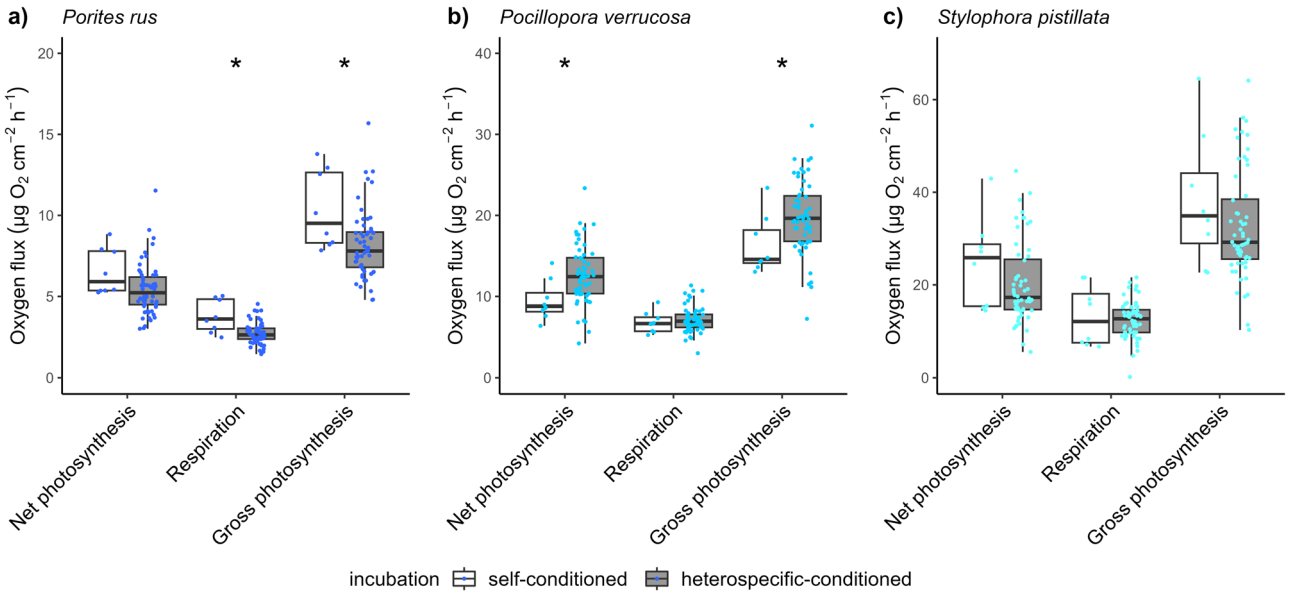

Fig. 1 Productivity of stony coral species in response to contact-free stimuli. Net photosynthesis, respiration and gross photosynthesis of *Porites rus* (**a**), *Pocillopora verrucosa* (**b**), and *Stylophora pistillata* (**c**) in self-conditioned (empty) and heterospecific conditioned seawater (filled). Data are displayed as boxplots with raw data points; lines indicate medians, boxes indicate the first and third quartile, and error bars indicate ± 1.5 interquartile range. Significant differences indicated as $^*p < 0.05$.

with the highest respiration found in incubations with the macroalgae *Caulerpa* sp. and *Halimeda* sp. and the lowest for *Sinularia* sp. and *A. muricata* (Fig. 3b).

Long-term effects of contact-free stimuli on stony coral productivity (Experiment 2). We detected the long-term effects of contact-free stimuli of monoculture or polyculture conditions on the productivity of stony corals. Similar to the immediate effects we observed in Experiment 1, the direction of the effect was dependent on the incubated coral species. *Acropora muricata* maintained similar photosynthesis and respiration between monoculture and polyculture, but decreased calcification rate and symbiont density in polyculture (Fig. 4, Supplementary Table 5). *Montipora digitata* maintained similar productivity between monoculture and polyculture for all parameters. In contrast to the short-term decreased productivity, *P. rus* increased net photosynthesis and calcification rate in long-term polyculture, consistent with a positive trend in symbiont cell density (Supplementary Table 5). *P. verrucosa* generally increased photosynthesis in polyculture, but not calcification (Supplementary Table 5). Similar to the lack of immediate effects in Experiment 1, the productivity of *S. pistillata* remained unaffected by long-term culture conditions (Fig. 4). Interestingly, none of the incubated stony corals showed an effect of long-term culture conditions in respiration.

Discussion

The importance of species diversity and composition for ecosystem productivity often exceeds the significance of environmental parameters such as climate or nutrient availability[1]. Here, we quantified the effects of neighbor organisms on the productivity of stony coral species in a complementary short- and long-term approach. By systematically excluding confounding biological and physical factors, our approach provides experimental proof that contact-free stimulation affects stony coral productivity at the level of the individual organism. The direction and magnitude of these changes largely depended on the responding species, with a minor role of the interaction partner.

Our initial hypothesis that coral productivity would primarily be modulated by the identity of the neighboring organisms could not be confirmed here. This hypothesis was based on extensive documentation that some interaction partners produce secondary metabolites[28–30] and negative effects of contact-based interactions[10,20,21]. Instead, each stony coral species had a unique and characteristic productivity response that was consistent across a range of neighboring organisms and stimuli in our experiments. *Pocillopora verrucosa* increased photosynthetic rate as an immediate and a long-term response to heterospecific stimuli, with consistent effects caused by contact-free heterospecific interactions. This species is competitive and can dominate communities[31], which is supported here by an increase in photosynthetic productivity in polyculture. The diversity-induced increase in photosynthesis, however, was not accompanied by an increase in symbiont density or calcification rate, which might have been expected based on its diversity-induced mass increase in the field[24]. In contrast, *P. rus* reacted with a decrease in photosynthetic rate as an immediate response to heterospecific contact-free stimuli while it increased photosynthetic and calcification rates in long-term polyculture. This adaption of productivity over time has been observed before (as cited in Rinkevich and Sakai 2001[32]). In their study, *P. rus* was weaker than *Porites lutea* (Edwards and Haime 1860) in the short-term, but stronger in the long-term. *P. rus* has also been identified as a dominant species in interaction with other *Porites* species with a tendency to overgrow them[33] and to colonize recently disturbed habitats[31]. In addition, such shifts in strategy within individuals over time have been described for coral early life stages, where the presence of conspecifics increased survival during settlement, while the presence of heterospecifics increased survival after settlement[34].

Stylophora pistillata and *Montipora digitata*, a weedy and a competitive species[31], respectively, maintained stable productivity in all treatments. *Stylophora pistillata* is a model organism to study allogeneic and xenogeneic responses[35] with numerous studies demonstrating that it reacts differently to allogeneic than to xenogeneic challenges[36–38]. However, these reactions do not seem to translate into direct productivity responses in this species.

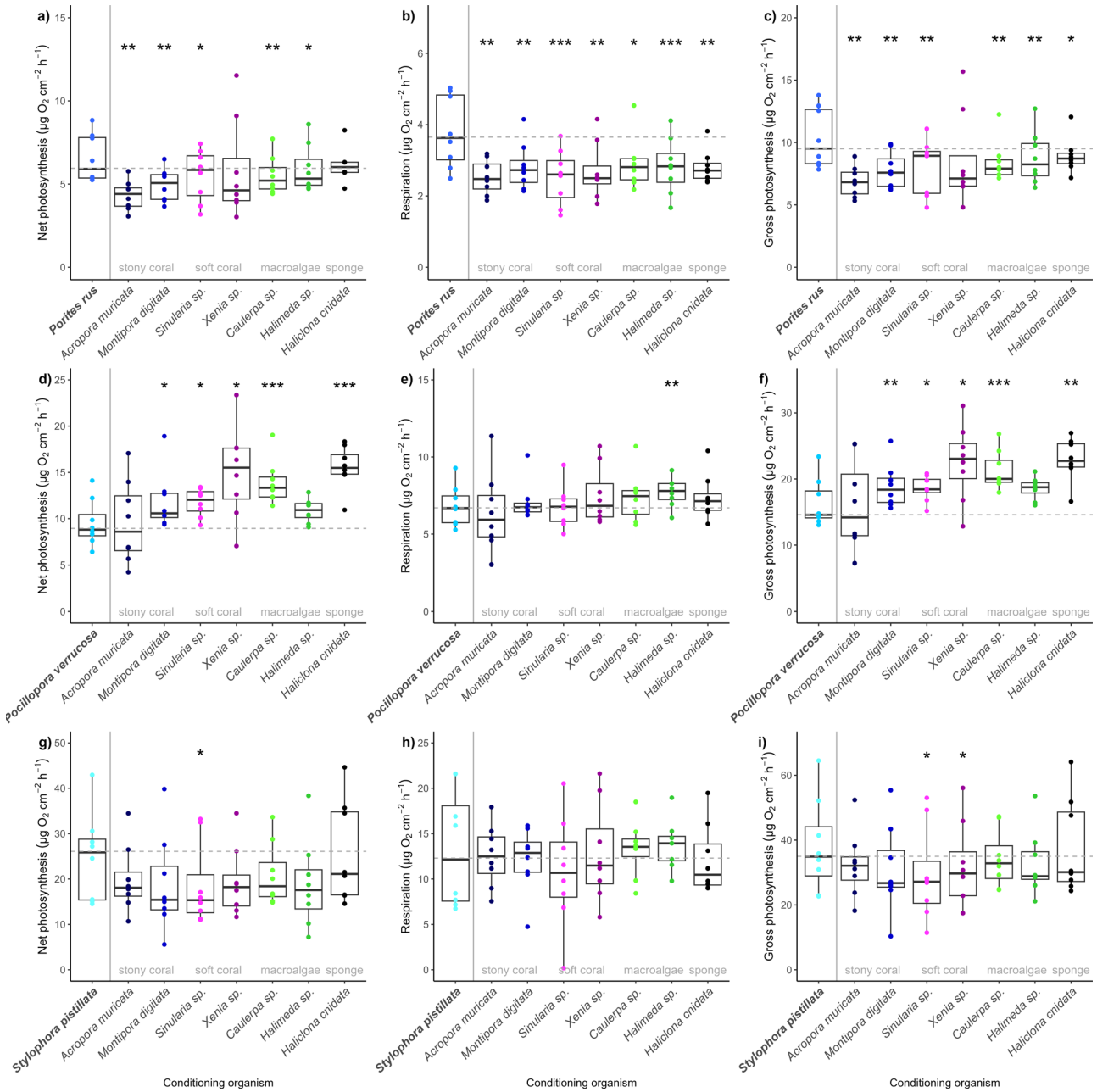

Fig. 2 Productivity of stony coral species in response to contact-free stimuli depending on the interaction partner. Net photosynthesis (**a, d, g**), respiration (**b, e, h**) and gross photosynthesis (**c, f, i**) of the three incubated coral species (*P. rus* (**a**–**c**), *P. verrucosa* (**d**–**f**) and *S. pistillata* (**g**-**i**)) in self-conditioned (left of solid line) and heterospecific conditioned seawater (right of solid line). Heterospecifically conditioned incubations are divided according to the respective interactions partner used. Data are displayed as boxplots with raw data points; lines indicate medians (dotted line elongates median to illustrate increasing or decreasing effects of the different conditioning organisms), boxes indicate the first and third quartile, and error bars indicate ± 1.5 interquartile range. Significance levels between each heterospecific stimulus compared to the self-conditioned control are indicated as * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Similarly, *M. digitata* induced negative responses in other stony corals in our study, but the species itself seemed largely unaffected by such stimuli. *Acropora muricata* also maintained stable photosynthesis and respiration, which is surprising given the significant decrease in symbiont density and calcification in long-term polyculture. *A. muricata* can be classified as competitive, with efficient resource use and the capability to dominate communities in productive environments[31], where it maintains high calcification under polyculture settings[24]. However, our results match those of McWilliam et al. 2018[18], in whose study the genus *Acropora* thrived in monoculture.

The productivity response of stony corals was primarily influenced by the coral itself and not by the neighboring organisms. Nonetheless, the neighboring organisms modulated coral productivity in a surprisingly consistent, yet more subtle, pattern across coral species. *Acropora muricata* negatively influenced the photosynthesis of all stony coral species. Accordingly, the polyculture set-up for conditioning may thus have succeeded in stimulating the release of aggressive metabolites in this species. But this result stands in contrast to our initial expectation of this species to boost other species as best performer in a previous experiment (Vetter et al. personal communication). This

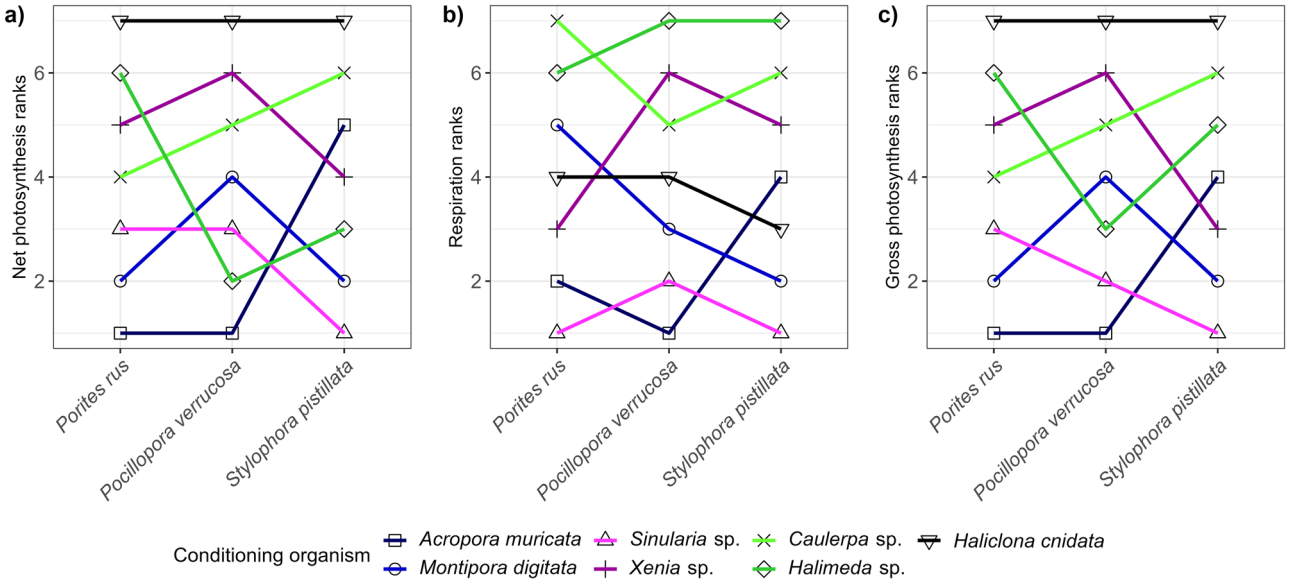

Fig. 3 Effect ranks of conditioning organisms for productivity parameters across coral species. Each conditioning organism was given a specific rank for net photosynthesis (**a**), respiration (**b**), and gross photosynthesis (**c**), with low ranks (1-2) indicating worst influencers and high ranks (6-7) indicating best influencers of stony coral productivity.

discrepancy might be the result of differences in experimental design and the release of inhibiting stimuli, which were previously unaccounted for. The effect of *A. muricata* was even more detrimental than that of *M. digitata*, our candidate as worst influencer. Interestingly, these two stony coral species caused the largest decrease in productivity in our experiments. It is surprising that the stony corals had such a strong negative influence on the productivity of the responding stony corals compared to the other organism groups, suggesting the presence of strong competitive interaction mechanisms within the stony coral group.

The sponge *H. cnidata* consistently invoked the highest productivity relative to other conditioning treatments; even in *P. rus* where trends overall were negative. Because of its documented high bioactive potential and storage of functional nematocysts[30], we expected it to negatively affect stony coral productivity. One possible explanation for its positive effect may be a suspected symbiosis with Cnidaria[39], making its interactions in the reef more complex, and requiring follow-up work. Alternatively, increased productivity by corals could also be a defense mechanism, to avoid competition by the sponge.

We predicted that the soft corals would negatively influence the productivity of stony corals, due to their known excretion of secondary metabolites[28], and their ability to quickly overgrow coral colonies on degraded reefs[40]. This negative effect was confirmed for *Sinularia* sp. in interaction with *P. rus* and *S. pistillata*, in which it induced the strongest effect of all organisms. The species *Sinularia flexibilis* can produce and release the toxic terpenoids flexibilide and dihydroflexibilide[14], which might be partly responsible for the sharp decline in photosynthetic productivity of the stony corals studied. In *P. verrucosa* we noted positive productivity effects of the species in intermediate ranges along with the macroalgae. The macroalgae *Caulerpa* sp. has been shown to aggressively overgrow coral colonies[41] probably enabled by secondary metabolites[29]. The order Caulerpales is known to produce a range of linear terpenoid metabolites for antiherbivore defense, like Caulerpenyne[29]. Since our conditioning organisms were kept in polyculture with grazing fishes the production of these toxins might have been triggered and subsequently affected the coral species during incubations. However, the contrasting effects of *Caulerpa* sp. on the corals with increased productivity in *P. verrucosa*, no change in *S. pistillata*, and decreased productivity in *P. rus* indicate that these compounds might be more relevant in contact-based interactions than in those without contact tested here. *Halimeda* sp. can reduce coral growth rates and cause tissue mortality[42]. This genus can produce diterpenoids as feeding deterrents, mostly halimedatetraacetate, which can be turned into the more toxic halimedatrial when the algae is injured[43], as could have been induced by the grazing fishes in our polyculture tank. Because, some coral species can defend themselves against *Halimeda* sp.[44], the expectation was that *Halimeda* sp. would be less aggressive towards the stony corals than *Caulerpa* sp.. However, we did not detect a large species-specific effect between the two macroalgae.

The contact-free interactions may cause changes in the associated microorganisms of stony corals, which then affect productivity, but the mechanisms behind this remain to be investigated[42]. Also not all detrimental effects between reef organisms are mediated through secondary metabolites explicitly tested in this study. Possible other inhibitory mechanisms may be mediated through processes including overgrowth[11], asexual recruitment[45], whole colony movement[46], or regeneration[47], which may lead to differential ecological outcomes in the field.

Our study showed that corals perceive neighbor organisms without physical contact via traces left behind in the water, even if they do not occupy the same space. Thus, the presence of another species must be transmitted with chemical signals via the water as part of so-called biocommunication[13,48]. These signals are released into the water column by marine organisms from both, the host and the associated microorganisms, as secondary metabolites[13,29,30,49]. The effects of these secondary metabolites may be positive, neutral, or negative[13]. For instance, secondary metabolites can act as inhibitory allelochemicals[15,36,50], with diverse roles in chemical signaling and contact-free competition[23] from repellents to toxins[16]. However, some secondary metabolites also have positive effects[13,48]. For instance, indole-based compounds, such as indole-3-acetic acid, which may be released by various marine organisms and have been studied for their photosynthesis-enhancing effects and promoting cell division in phytoplankton[51,52]. The presence of indole-3-acetic acid has recently been documented from coral reef organisms[53] and could

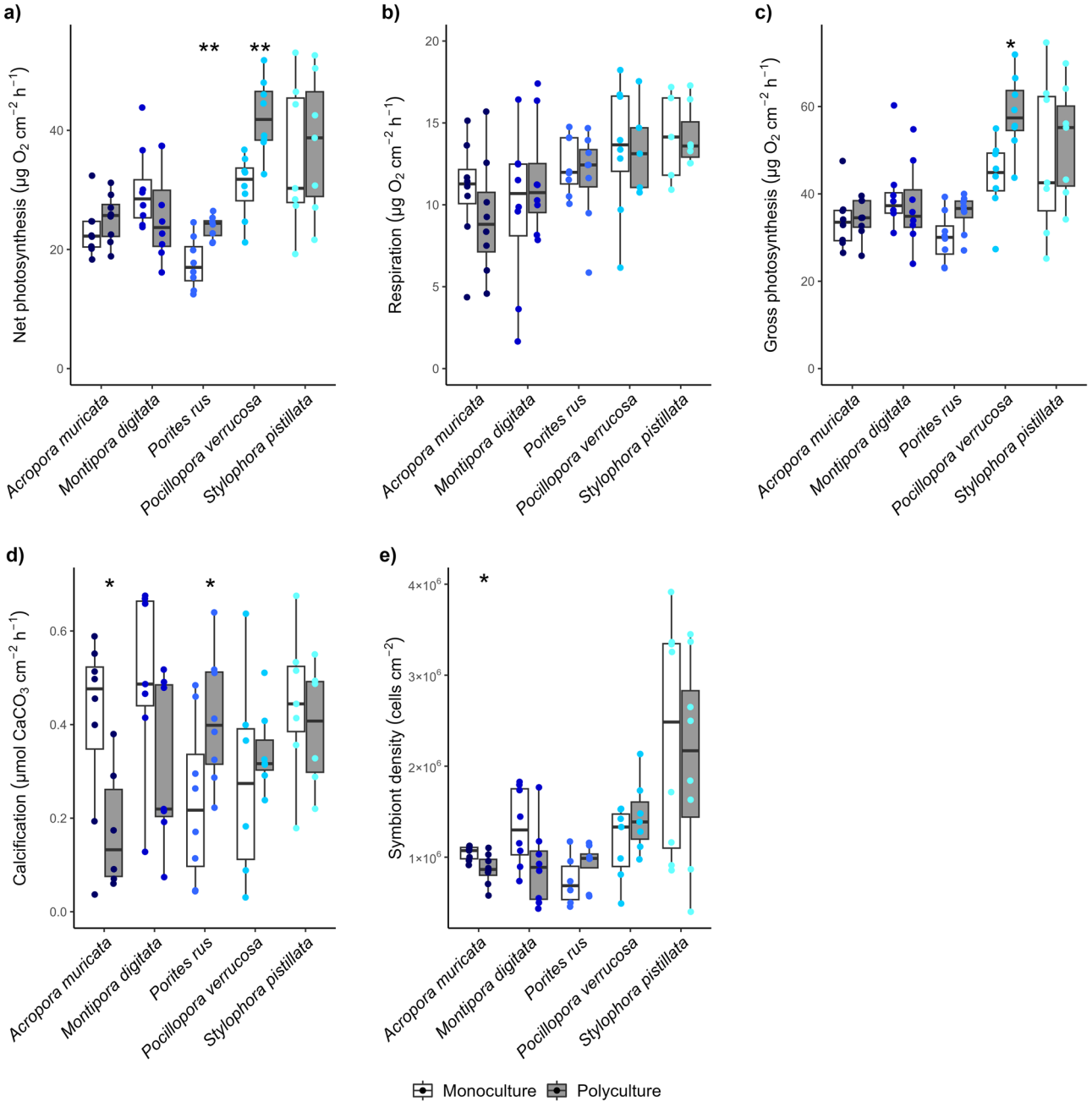

Fig. 4 Productivity of stony coral species in response to long-term contact-free stimuli. Net photosynthesis (**a**), respiration (**b**), gross photosynthesis (**c**), calcification (**d**), and symbiont cell densities (**e**) of five incubated stony coral species in monoculture (empty) and polyculture (filled). Data are displayed as boxplots with raw data points; lines indicate medians, boxes indicate the first and third quartile, and error bars indicate ± 1.5 interquartile range. Significance levels are indicated as * $p < 0.05$; ** $p < 0.01$.

thus potentially explain enhanced photosynthetic productivity of corals in our study.

Stony corals, soft corals, macroalgae, and sponges produce a plethora of secondary metabolites which constitute a species-specific profile and initial studies have shown that they are exuded into the environment surrounding the organisms[53]. However, we do not yet understand well when, how, and which secondary metabolites are emitted by coral reef organisms. This information is urgently needed to disentangle the cues that underlie the physiological modulation demonstrated herein, which may ultimately be based on the presence of particular metabolites or classes of metabolites, a metabolite concentration threshold, or more complex patterns.

Our data show that corals sense the presence of neighboring organisms without physical contact and translate this into a physiological response. Presumably, the resulting changes in productivity might be modulated through a historecognition system that allows stony corals to distinguish between self and non-self[48,54,55]. To date, it is assumed that the historecognition system exclusively recognizes the presence of either self or of non-self attributes[56].

As each species consistently changed its physiology in response to all conditioning organisms, our data suggest a recognition mechanism based on self-recognition[57]. Thus, all colonies have a unique histocompatibility identity. In *Hydractinia*, two linked genes enable self/nonself-recognition among conspecifics through

the binding of identical allorecognition molecules[58,59]. This mechanism remains to be confirmed in stony corals. On the other hand, the unique histocompatibility is perceived by other colonies as non-self[38], which leads to the here-observed, identical response of the perceiving species in all heterospecific interactions. Because the conditioning species also produced a minor but consistent effect across the three responding coral species, there also appears to be a form of non-self-recognition and thus an individualization of effects in response to different nonself attributes[57]. These histocompatibility responses require an allorecognition system, which can detect subtle differences among genetically different conspecifics[60]. Indeed, the distinction of different non-selves by cnidarians has already been observed in various stony coral species[19,38,57,61]. Detailed studies suggest that the functioning of the defence system might differ from those involved in recognition[62,63], which remain to be uncovered.

Our data thus show two co-occurring forms of discrimination for both self and non-self attributes, which were previously assumed to be mutually exclusive in each organism[56]. Accordingly, a combined mechanism for discriminating for self and non-self may underlie, with recognizing self attributes as the more dominant mechanism and non-self attributes as the secondary mechanism.

Previous research has shown that the biodiversity of a system and its community-level productivity are linked[64]. Our results further indicate that the productivity of each species in such systems is individually modulated. Thus, biodiversity loss in reef ecosystems may result in indirect effects on community composition through species-specific modulation of productivity. The loss or changed distribution patterns of species alters interactions between species and therefore indirectly ecosystem productivity. Loss of biodiversity may disproportionately benefit some species, as for example *A. muricata* in our study with higher productivity in low diversity settings, while species such as *P. verrucosa* with strong diversity-driven enhancement of productivity, would be disproportionately disadvantaged. The species-level modulation of productivity may thus contribute to changes in species assemblages after disturbance.

Our data provide important insights for reef restoration, as they demonstrate potential positive biodiversity effects on a per-species base. These could be used in restoration efforts by combining species in nurseries and out-planting that boost each other's productivity and thus likely restoration yields. The idea of such strategic species combinations to increase production follow long-known principles in crops and gardening, for which antagonistic and beneficial species combinations are well established[65,66]. Our data further suggest that the inclusion of non-coral species such as *H. cnidata* in nurseries could boost production across all target species. However, many questions on the effectiveness and economics of these productivity interactions remain to be addressed for their practical application. For instance, what are the productivity effects between typical restoration species and how can they be arranged best in the field to optimize productivity? How does the space needed to include a non-target species that increases yields relate to the space needed to yield that same productivity without including it, and how do such mixtures affect stony coral health in the long-run?

Conclusions

This study demonstrates that the productivity of stony corals is dependent on neighboring organisms, which have an influence even without physical contact. Changes occur at the level of the individual stony coral with the responding species as the main driver of productivity changes. In addition, the influencing species also showed a consistent effect, with subordinate weight for the overall response. The ability to perceive other organisms without physical contact probably arises from a historecognition system, which allows the coral to distinguish self from non-self. Due to the observed two-sided effects on productivity, our data suggest that stony corals are both self- and non-self-recognizing, with self-recognition as the more dominant mechanism. Chemical signaling and secondary metabolites thus play a crucial role in contact-free interactions and by that in productivity modulation. Biodiversity loss may therefore indirectly affect benthic community composition through species-specific modulation of productivity and uneven effects that benefit some species while others are inhibited. Our data provide important insights for reef restoration approaches, as they demonstrate potential positive biodiversity effects on a per-species base that could be harnessed to increase yields for nursery species. Further research should determine which substances are emitted by organisms under which biodiversity conditions and how these substances are translated into a physiological response by the individual organism.

Materials & Methods

To investigate effects of neighbor organisms on the productivity of stony coral species, we conducted two aquarium experiments monitoring the immediate and long-term response of stony corals in the *Ocean2100* coral aquarium facility of Justus Liebig University Giessen, Germany.

Experiment 1: Immediate effects of contact-free stimuli by sessile organisms on stony coral productivity. To identify immediate contact-free effects of stimuli by sessile reef organisms on stony coral productivity, we conducted a 10-week laboratory experiment in March 2021 (Fig. 5). Net photosynthesis and respiration of three stony coral species from two different families were measured after contact-free stimulation with conditioned water from seven coral reef organisms, further referred to as conditioning organisms. The conditioning species included two stony coral species, two soft coral species, two macroalgae species, and one sponge species.

Incubated species. To assess changes in productivity in response to contact-free stimuli, we measured photosynthesis and respiration of three stony coral species: *Porites rus* (Forskal 1775) from the Poritidae family, and *Pocillopora verrucosa* (Ellis & Solander 1786) and *Stylophora pistillata* (Esper 1797) from the Pocilloporidae family. We based the selection of these species on data from Vetter et al. (personal communication), in which the productivity of nine stony coral species was investigated. The three species were selected as what we hereafter refer to as incubated species for this experiment, based on their intermediate and variable performance in response to neighboring organisms (Supplementary Table 1). We hypothesized that the productivity of these species may react positively or negatively depending on the identity of the conditioning organism.

We produced two replicate fragments from four genetically different colonies from each stony coral species ($n = 8$) with an angle grinder (Multitool 3000-15, Dremel, The Netherlands) and let them heal for eight weeks before the experiment. All fragments were held in monoculture tanks during acclimation and experimental period, with each tank only containing fragments of the same species to keep them naïve to biological stimuli. Additional fragments of the incubated species were kept in the monoculture tank, for the self-conditioned control. All organisms for the experiments were cultured at 26 °C, a light intensity of 200 µmol photons m^{-2} s^{-1}, and salinity of 35. In order to avoid interactions during the experiment procedures, coral fragments

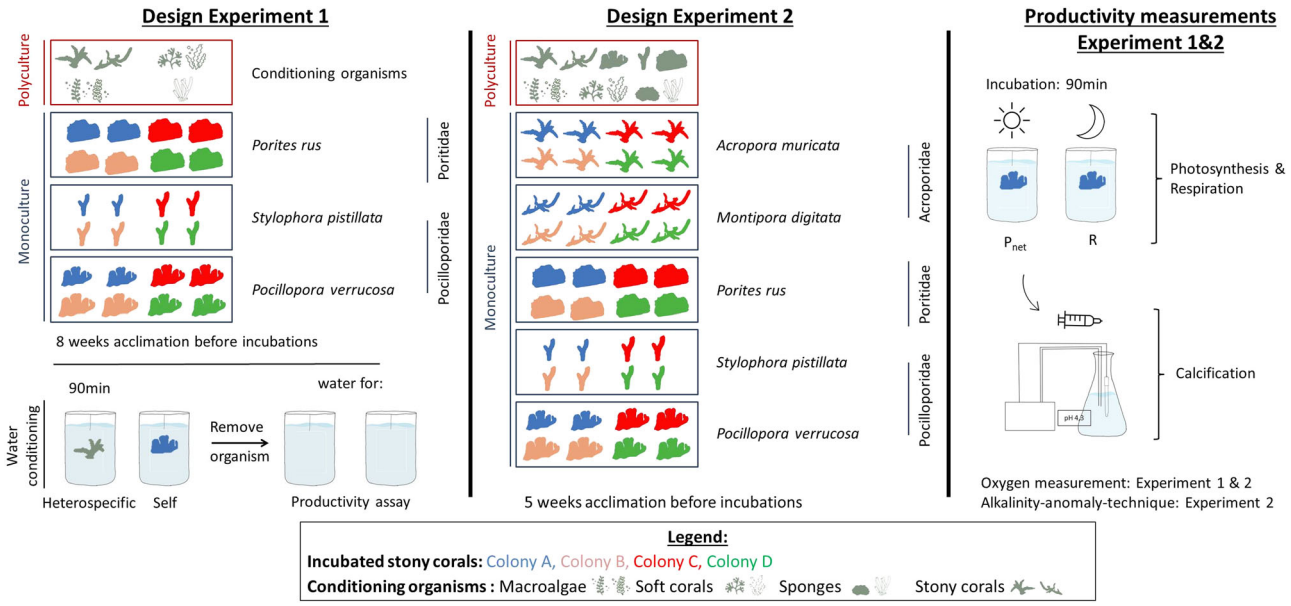

Fig. 5 Experimental design of the experiments and subsequent measurements. Maintenance of stony coral species in monoculture and polyculture tanks with different sessile reef organisms for eight (Design Experiment 1) and five (Design Experiment 2) weeks before productivity measurements (Productivity measurements Experiment 1&2). Colors indicate genetically different colonies (blue, red, beige, green) of the incubated species. Conditioning species and polyculture species are grey, blue indicates monoculture tanks and red indicates polyculture tanks.

were handled on their suspension lines and never touched directly. In addition, nitrile gloves were worn at all times, even when only in contact with water, so that the corals were not exposed to unintended contact-free interactions with the human skin.

Conditioning organisms. We preconditioned the artificial seawater for incubations with other sessile reef organisms from four functional groups including stony corals, soft corals, macroalgae, and sponges. We chose the stony coral species *Acropora muricata* (Linneaus 1758) and *Montipora digitata* (Dana 1846) from the Acroporidae family based on their performance as best and worst performer, respectively in the experiment by Vetter et al. (personal communication) (Supplementary Table 1). We expected that stimuli by *A. muricata*, which was present in only high-performing coral assemblages previously, would positively influence the productivity of the incubated organisms, while stimuli by *M. digitata* would show a negative effect on productivity because of its previous presence in the least productive coral assemblages. Furthermore, we used two soft coral species from the order Alcyonacea, *Sinularia* sp. (May 1899) and *Xenia* sp. (Lamarck 1816), two macroalgae species, *Caulerpa* sp. (Lamouroux 1809) from the Caulerpaceae family and *Halimeda* sp. (Lamouroux 1812) from the Halimedaceae family, and the stinging black sponge *Haliclona cnidata* (Schellenberg, Reichert, Hardt, Schmidtberg, Kämpfer, Gläser, Schubert & Wilke 2019).

For maintenance, we kept all conditioning organisms (one genotype each) in a polyculture tank in the aquarium facility. We chose these polyculture conditions to stimulate the bioactive potential of the conditioning species, since increased diversity of the community has previously shown to stimulate the production of secondary metabolites in reef organisms[67,68].

Water preparation for contact-free stimuli (Experiment 1). To condition the water before incubations, we transferred 2 ×17 l of seawater from an empty and clean holding tank without organisms, connected to the main recirculating system, to a separate tank. Then, we transferred fragments from one of the conditioning species (*A. muricata, M. digitata, Sinularia* sp., *Xenia* sp., *Caulerpa* sp., *Halimeda* sp., or *H. cnidata*) per day into this water for 90 min before the incubations (Supplementary Table 2). The conditioning of the seawater was carried out in the light (200 µmol photons m^{-12} s^{-1}) for photosynthesis measurements and in the dark for respiration measurements. During preconditioning the water was aerated to keep dissolved oxygen values comparable between runs. We used self-conditioned water, with fragments of the same coral colony preconditioned for 90 min, as control.

Experiment 2: Long-term effects of contact-free stimuli on stony coral productivity. To test long-term effects of contact-free stimuli by sessile reef organisms on coral productivity, we conducted a 5-week experiment in January 2022, in which organisms were either held in single-species monoculture tanks or together in a polyculture tank. At the end of the experiment, we measured photosynthesis, respiration, calcification, and symbiont cell density of corals from both culture settings in neutral conditions, i.e., in nonpreconditioned seawater from an empty tank. We conducted measurements of the five stony coral species from Experiment 1 (*A. muricata*, *M. digitata*, *P. verrucosa*, *P. rus*, *S. pistillata*). The polyculture tank contained these species and additional sessile reef organisms to increase the potential diversity of contact-free stimuli in this treatment. The additional species were the same as in Experiment 1 (soft corals: *Sinularia* sp., *Xenia* sp., except for one macroalgae species: *Caulerpa* sp., *Peyssonnelia* sp. (Decaisne 1841) instead of *Halimeda* sp., sponge: *H. cnidata*) and an additional sponge species (*Tethya* sp. (Lamarck 1815)). We selected four genetically different colonies from each stony coral species, of which we prepared four ($n = 16$) fragments. We placed eight fragments of each species in a monoculture tank for healing and acclimation, and eight fragments in a polyculture tank together with the other reef organisms for five weeks (Fig. 5).

Productivity measurements (Experiment 1 & 2). The incubations for both experiments followed the same procedures. On each day, we performed a light incubation (net photosynthesis)

directly followed by a dark incubation (respiration, Fig. 5) of individual stony coral fragments. We conducted incubations in 1l jars, which were sealed airtight and air-free during incubations. At the start of each incubation, we determined oxygen concentration, temperature, and salinity of the water (Experiment 1: water pre-conditioned by one conditioning organism; Experiment 2: neutral water from an empty tank) with a multiparameter probe (Xylem Analytics, Multi 3620 IDS Set, Germany). We used two control incubations per day without coral fragments to determine the biological activity of microorganisms in the water. In Experiment 1, we carried out additional control incubations in self-conditioned water. In Experiment 1 each fragment was incubated once with each interaction partner and in the self-conditioned control, in Experiment 2 each fragment was measured once. Light levels of 190-210 µmol m^{-2} s^{-1} and a temperature of 25.5 ± 2.2 °C (± SE) were maintained during 90min incubations. Each incubation jar contained a stirring bar creating a current of 7 ± 0.5 cm s^{-1}[69]. After each experimental day, all containers were rinsed with deionized water and dried to avoid build-up of residues.

Coral photosynthesis. To calculate net photosynthesis and respiration, we measured O_2 change during light and dark incubations, respectively, normalized to coral surface area (cm^2) and incubation time (h). To obtain the productivity of the fragment, we corrected all photosynthesis and respiration values with the average production of the controls for each day. To calculate gross photosynthesis, we summed up the values of net photosynthesis and respiration.

Coral calcification. During light incubations, we measured coral calcification in the long-term monoculture and polyculture experiment using the total alkalinity anomaly technique[70]. To measure Total Alkalinity (TA) we used a potentiometric titration with 0.1 N HCl (TitroLine® 7000, SI Analytics™, Germany) and a glass electrode (Pt1000, SI Analytics™, Germany). We took 50 ml water samples at the beginning and at the end of each light incubation. These samples were stored in the dark and measured within 5 h at 20 °C. For comparable measurements we calibrated the pH electrode daily (slope from 98 to 99%). We calculated TA via the Gran Alkalinity Approximation (Formula 2) with the first Gran function (Formula 1).

$$F_1 = 10^{-\mathrm{pH}} \times (V_s[\mathrm{ml}] + V_t[\mathrm{ml}]) \quad (1)$$

F_1 is the gran approximation calculated from values of V_t (volume of titrant) and pH values (output by the titrator) and V_s (sample volume).

$$\mathrm{TA}\,[\mathrm{mmol\,l^{-1}}] = \frac{\mathrm{Normality\ HCl}\left[\mathrm{equiv\,l^{-1}}\right] \times Ve\,[\mathrm{ml}] \times 1000}{Vs\,[\mathrm{ml}]} \quad (2)$$

TA is calculated with Normality HCl, which stands for the hydrochloric acid concentration multiplied with V_e representing F_1 calculated in Formula 1 divided by sample volume (V_s) (Formula 2).

We used TA values to determine calcification rates with the alkalinity anomaly method, as described in Schneider and Erez[71] (Formula 3).

$$\mathrm{G}\,[\mu\mathrm{mol\,CaCO_3\,cm^{-2}\,h^{-1}}] = \frac{\frac{\Delta \mathrm{TA}}{2} \times (V[\mathrm{l}]) \times \text{water density}\,[\mathrm{kg\,l^{-1}}]}{\mathrm{Surface}\,[\mathrm{mm^2}] \times T\,[\mathrm{h}]} \quad (3)$$

To calculate calcification rate G, we divided the TA difference between start and stop by 2. We multiplied V (Volume of the glass jar minus all non-biological parts) with the water density and divided the sum by the sum of the respective coral surface area and the duration of the incubation. As correction of calcification, we used the respective seawater controls.

Coral surface determination with 3D scanning. In both experiments, we normalized all productivity data to the surface area of the stony coral fragments. For this, we created 3D models with the 3D scanner Artec Spider (Artec Group 2009) using the software Artec Studio 9.2.3.15 (Artec 3D, Luxembourg) following Reichert et al.[72]. Briefly, we used the following settings for scanning: brightness = medium, sensitivity = medium, number of frames per second = 8. We calculated each scan (maximum value of registration error <0.5) in Artec Studio with a final mesh size of 0.2 mm using ´fine serial registration´, ´global registration´, ´outlier removal´ and ´sharp fusion´ (by radius 0.5). For minor corrections we used the eraser, followed by a ´sharp fusion´ (watertight). We then exported the meshes as wavefront (´.obj´) files to the program Meshlab Visual Computing Lab-IST-CNR (v1.3.4 BETA, 2014) to calculate the surface area with the 'compute geometric measures' tool.

Symbiont cell counts. We determined the cell density of the endosymbiotic microalgae (family Symbiodiniaceae) in the coral tissue, to test its relation to changes in coral productivity due to long-term mono- or polyculture. At the end of Experiment 2, we froze all coral fragments (−20 °C) and isolated the symbiont cells following Zamoum and Furla[73]. To do this, we placed the fragments in 1 molar NaOH solution at 35 °C and shook them every 15 min for 1 h. Subsequently, we removed the bare coral skeletons and centrifuged the solutions at 2,958 g for 5 min. We discarded the supernatant and washed the pellet twice by resuspending in 10 ml of tap water, followed by centrifugation. To achieve a cell density of 10-50 cells per group square for counting with a Thoma hemocytometer (Marienfeld GmbH, Germany), we adjusted the final volume of the cleaned symbiont solution (8-12 ml). On each half of every slide, we counted five group squares for a total of three slides, resulting in six repetitions and a sum of 30 group squares per fragment. We used the mean of the six replicates to calculate the symbiont density and normalize to coral surface area.

Statistical analysis. We performed all statistical analyses in R statistical environment (v.4.0.2, R Core Team 2020[74]) using the tidyverse packages[75]. In Experiment 1, we compared the overall effect of heterospecific conditioning on coral productivity (net photosynthesis, respiration, gross photosynthesis) to the self-conditioned controls using independent samples T-tests with Bonferroni correction. When data were not normally distributed (Shapiro-Wilk-Test) or variance was unequal (Levene-Test), we log or square-root transformed the data or analysed it with a Wilcoxon rank-sum test if assumptions could not be met by transformation. Subsequently, we examined the effect of the individual conditioning organisms on stony coral productivity for each incubated species-conditioning organism pairing separately using paired T-tests after normal distribution (Shapiro-Wilk-Test) of the mean difference between pairs was confirmed. When normal distribution could not be confirmed, also not with a log or square-root transformation, we performed Wilcoxon signed-rank tests instead. For the conditioning organisms, we aimed to determine the organism that had the strongest negative effect on productivity hereafter referred to as 'worst influencer' and the organism with the strongest positive effect on productivity hereafter referred to as 'best influencer'. To further test the recurrence of their effects across incubated species, we ranked the mean value in each productivity parameter. The conditioning

organism with the consistently highest mean value was designated as best influencer, while the conditioning organism with the lowest mean value was the worst influencer.

With the data from Experiment 2, we performed individual paired T-tests with Bonferroni correction per stony coral species between long-term monoculture and long-term polyculture for net photosynthesis, gross photosynthesis, respiration and calcification. Normal distribution (Shapiro-Wilk-test) of the mean difference between pairs was confirmed for all data, except for respiration, for which we performed Wilcoxon signed-rank tests instead. For symbiont cell densities, we performed Wilcoxon rank-sum tests, since normal distribution and homogeneity of variance could not be confirmed.

Data availability

Raw data (oxygen measurements, titrations and symbiont counts) generated and analysed during the current study are available in GitHub 'Contact-free-impacts-of-sessile-reef-organisms-on-stony-coral-productivity', [https://github.com/KaraEngelhardt/Contact-free-stimuli][76].

Code availability

R scripts used for this study are available in GitHub 'Contact-free-impacts-of-sessile-reef-organisms-on-stony-coral-productivity', [https://github.com/KaraEngelhardt/Contact-free-stimuli][76].

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Author contributions

K.E.E., J.V., F.W.-Z., and M.Z. conceived the study and designed the experiments. K.E.E., J.V., F.W.-Z., A.D., F.M.P., H.R., I.S., and M.S. collected data, K.E.E. and F.W.-Z. analyzed and curated data. K.E.E. and M.Z. wrote and revised the manuscript. M.Z. provided research materials and logistics. J.V. and F.W.-Z. contributed equally. All authors read and approved the manuscript.

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Competing interests

The authors declare no competing interests.

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