Research

Author for correspondence:
Mohsen Kayal
e-mail: mohsen.kayal@ird.fr

The war of corals: patterns, drivers and implications of changing coral competitive performances across reef environments

Mohsen Kayal[1,2] and Mehdi Adjeroud[2,3,4]

[1]ENTROPIE, IRD, CNRS, IFREMER, Université de la Nouvelle-Calédonie, Université de la Réunion, Noumea, New Caledonia
[2]Laboratoire d'Excellence 'CORAIL', Paris, France
[3]ENTROPIE, IRD, CNRS, IFREMER, Université de la Nouvelle-Calédonie, Université de la Réunion, Perpignan, France
[4]PSL Université Paris, USR 3278 CRIOBE - EPHE-UPVD-CNRS, Perpignan, France

MK, 0000-0003-3675-9855; MA, 0000-0002-6825-8759

Amidst global environmental changes, predicting species' responses to future environments is a critical challenge for preserving biodiversity and associated human benefits. We explored the original idea that coral competitive performances, the ability of corals to preempt ecological space on the reef through territorial warfare, serve as indicators of species' ecological niches and environmental windows, and therefore, responses to future environments. Our surveys indicated that coral performances varied with taxonomic identity, size and position along environmental gradients, highlighting complex interplays between life-history, warfare-strategy and niche segregation. Our results forewarn that growing alterations of coastal environments may trigger shifts in coral dominance, with the decline of major reef-building taxa like acroporids, and emphasize the importance of limiting human impacts for coastal resilience. Our empirical approach untangles the complexity of species' battle-like interactions and can help identify winners and losers in various communities caught in the interplay between ecological niches, environmental windows and global changes.

1. Introduction

Predicting how global environmental changes will affect species' performances in the future is crucial to anticipating biodiversity declines and defining sustainable management. However, large

uncertainties regarding species' responses and future conditions blur current predictions of ecosystem trajectory in future environments [1,2]. Finding effective metrics of species' responses to changing environments is key, particularly for vulnerable ecosystems in need of rapid intervention, and in developing and island nations where high reliance on natural resources exacerbates socio-ecosystem vulnerability [3–5]. This is particularly true with coral reefs, which support prolific marine life and coastal livelihoods yet stand at the frontline of declining ecosystems due to rapidly altering coastal environments [1,6–9]. Reef degradation from growing coastal development, pollution, fishing and climate change predominantly involves a gradual decline in coral abundance, composition and size, with the progressive loss of vulnerable species, particularly at sensitive life-stages, altering key ecosystem functions [7,10–13]. Recent demographic modelling approaches allow for characterizing these dynamics on reefs using fine-scale monitoring data [2,14–16]. However, only a few eminent sites, representing an infinitesimal proportion of reefs, benefit from the necessary level of quantitative knowledge of demographic processes, leaving out most coral reef ecosystems from such quantitative diagnosis.

As an alternative to using demographic modelling, we hypothesize that coral competitive performances, the ability of corals to preempt space on the reef substrate through territorial warfare, could be used as a proxy of species' ecological success in different environments. Competition for space and other limiting vital resources is a key process shaping ecological communities in coral reefs, notorious for biodiversity and biotic interactions, and where competition warfare can drive community shifts and ecosystem collapse in altered environments [17–19]. We stipulate that differences in competitive performances across environments can provide insights on species' ecological niches, optimal environmental windows and, therefore, potential response to future conditions.

On reefs, direct competition for space is ubiquitous where neighbouring organisms grow into physical contact, species inevitably engaging in warfare for survival and ecological dominance. On the front line (a.k.a. the battle zone), corals have the capacity to invade opponent territories by killing enemy living tissues in their vicinity. This battle predominantly takes two forms with either smothering by growing over (a.k.a. overgrowth) or disintegrating using specialized nematocyst-rich attack-tentacles (a.k.a. overreach), or a combination of the two (figure 1). In theory, the magnitude of killing varies with fixed characteristics of species life history such as attack mechanism, strength and reach [14,20–24], but also with additional processes that vary in time, space and across life-stages such as growth rates and metabolic states of corals [25–29]. As such, while a clear hierarchy of competitive dominance among coral species can be established in a given environment, competitive outcomes in fact appear spatio-temporally dynamic [30–34] and are therefore expected to differ in the future with changing reef environments. Because corals are slow-growing, habitat-forming species at the foundation of reef ecosystems, even small differences in corals' abilities to preempt reef space can have strong implications for reef ecosystem structure, functions and associated benefits for society.

We used observations of coral competitive interactions across the southwestern reef system of New Caledonia [35] as indicators of the capacity of coral species to prevail in different environments. The island nation is surrounded by large extents of biodiverse coral reefs, characterized by diverse habitats distributed along pronounced coast-to-ocean gradients associated with natural environmental variability locally amplified by human impacts [36,37] (electronic supplementary material, figure S1). The near shore is most exposed to terrigenous inputs of freshwater, nutrient and sediment, as well as locally strong anthropogenic impacts from coastal development, pollution and fishing, and undergoes higher environmental variation with seasons and weather conditions [38–41]. Moving towards the ocean, marked increases in water quality and diminishing human pressure are observed. Portions of the reefs are classified as UNESCO World Heritage sites due to their outstanding character for global coral reef conservation. Zonation in the relative abundance of coral species along the coast-to-ocean gradient indicates some degree of niche segregation among dominant taxa [37]. However, the ecological mechanisms underlying such spatial patterns largely remain to be comprehended. Because coral species are expected to occupy delimited ecological niches distinguished by environmental preferences [7,29,42], we tested whether the spatial distribution of ecological windows would be reflected in coral competitive outcomes. In general, a deeper understanding of coral competition can help a better characterization of coral life-strategies, which at this stage predominantly relies on qualitative assumptions of species competitive abilities based on taxonomic traits and demographic performances [28,43]. A better understanding of coral competition can also inform on the ecological processes underlying species coexistence and the exceptional biodiversity of coral reefs.

We illuminate our findings with analogies to warfare theory and lessons from human history to untangle the complexity of coral competitive interactions. The parallels are based on the premise that outcomes of coral competitive interactions on a reefscape, much like human war on the battlefield, depend on a multitude of
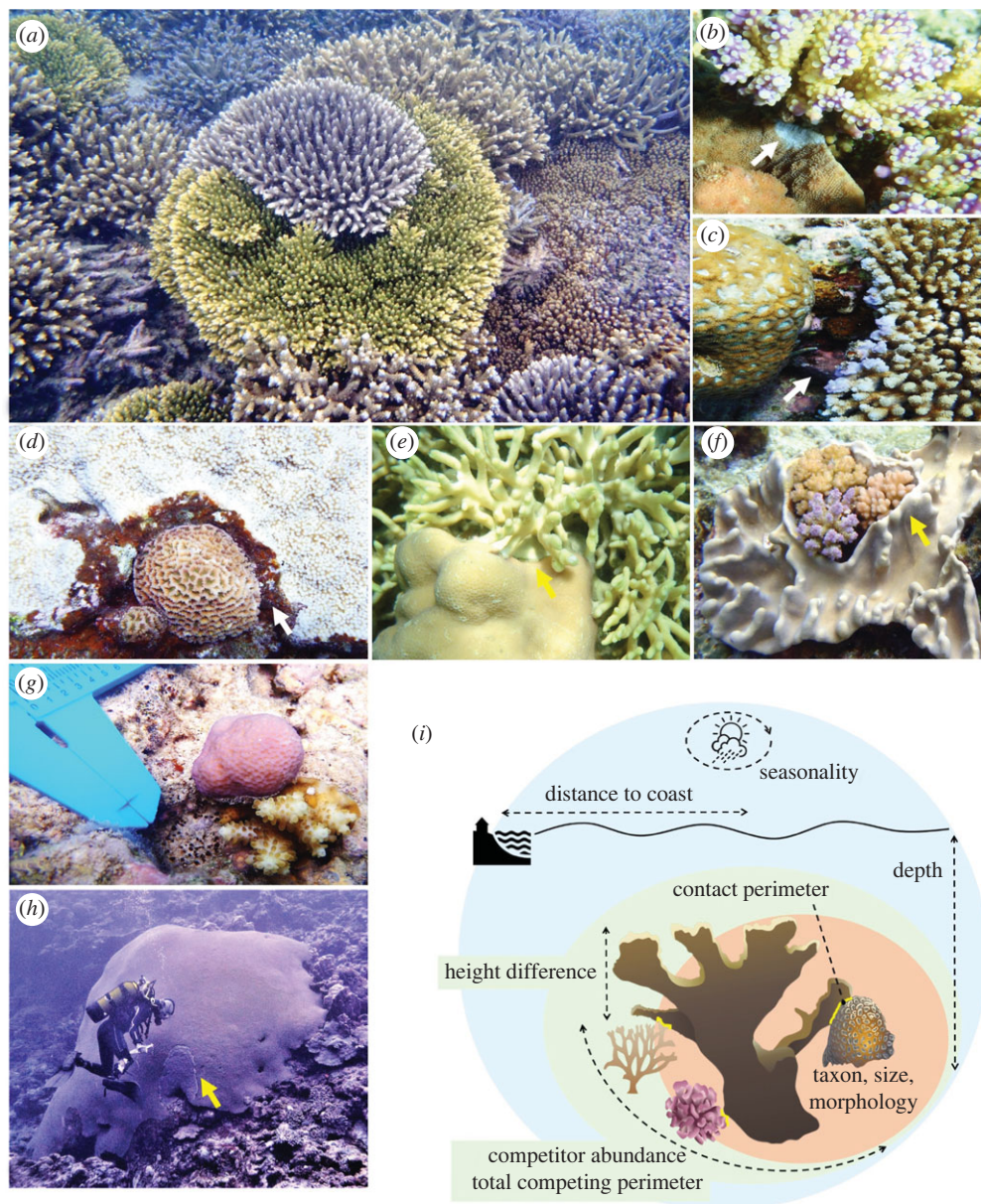
Figure 1. Photographs illustrating encountered coral competitive interactions (*a*–*h*) and schematic (*i*) indicating how they were characterized by taking into account a set of factors relating to individual organisms (beige), interactions (green) and environments (blue). By quantifying the dead zones left by sweeper attack-tentacles on opponent coral skeletons in the aftermath of competitive battles, overreach distances (white arrows) reflect short-term competitive outcomes resulting from recently deployed assaults (hours to months preceding observations). By contrast, given the slow growth of corals, overgrowth distances (yellow arrows) often integrate competitive interactions over several years. See electronic supplementary material, appendix S1 for further information, and electronic supplementary material, figure S2 for visualizations of the raw data.

factors, some intrinsic to the opponents' individual characteristics, others changing with ecological contexts related to interactions and environments. This effort facilitates understanding of the regulatory mechanisms involved in species as biologically distant to us as corals. We discuss the implications of our results for coral performances in the context of changing reef environments.

2. Methods

We evaluated coral competitive performances by inspecting natural occurrences of direct physical interactions among corals, as well as with other sessile benthic species (electronic supplementary

material, figure S2) [35]. Surveys were performed on 20 sites distributed along pronounced cross-shelf environmental gradients (electronic supplementary material, figure S1), and over a five-month period to capture seasonal variability with a shift from the warmer and humid summer conditions in January to the cooler and dry winter conditions in June (decreasing water temperature, 27–23°C). For each interaction haphazardly encountered, the taxonomic identities, morphotypes and three-dimensional size (length, width and height) of each organism (a randomly chosen coral designed as focal plus all of its direct competitors) were recorded, along with the contact perimeter characterizing the battle zone, and overreach and overgrowth distances as short- and long-term metrics of competitive outcomes (figure 1). Because coral demographic performances in survival, growth and reproduction vary with size [28,44], changes in coral abilities to defend their territories were related to species fitness (i.e. chances of ecological success). We focused specifically on direct competition for space (a.k.a. territorial war), leaving aside indirect competition for light, food, and other resources.

As competitive interactions regularly consisted of bilateral attacks, net overreach and overgrowth performances were calculated as the difference between the observed maximum conquered and ceded distances along the frontline. These measurements of net space gain in competitive battles differ from most studies on competition, which typically characterize species interactions as a simplistic binomial (win or loss) or trinomial (win or loss or standoff) outcome (e.g. [23,24,31–33]). Further characteristics of the interaction and environment that could also potentially influence competitive outcomes, such as distance to the coastal city Noumea, water depth, competitor abundance, total competing perimeter and differences in height among competitors, were also recorded and considered in data analysis (figure 1i; electronic supplementary material, table S1).

Because coral competitive outcome was expected to be influenced by various ecological factors that in concert shape species responses (figure 1i), we used generalized additive models to characterize changes in competitive outcome as a function of different candidate ecological descriptors (electronic supplementary material, table S1) in a nonlinear, multi-dimensional account [45]. Model parametrization was designed to capture a set of common ecological processes regulating coral performances, such as size and density dependence (e.g. covariates *Coral-size* and *Competitor-abundance*), as well as taxonomic deviations in such processes (e.g. interaction *Coral-size × Coral-taxon*) to account for evolutionary differences among species [28]. For example, we tested how coral overreach and overgrowth performances changed as a function of coral size (covariate effect *Coral-size*), and whether the size-dependent response differed among species (covariate–factor interaction *Coral-size × Coral-taxon*). Similarly, we tested whether coral size-dependent response varied with competitor abundance (covariate–covariate interaction *Coral-size × Competitor-abundance*). The degree of nonlinearity of each model term was optimized based on semi-parametric spline-penalization (see [28,46] for details), and non-significant model terms were sequentially excluded during the model selection process [45] (electronic supplementary material, figures S3 and S4). Among the multitude of possible models resulting from combinations of the explanatory variables, the models best describing competitive outcomes were identified using Akaike information criteria, a measure of trade-off between model performance and complexity [47]. A total of 103 and 144 different generalized additive models were tested during the model selection process for coral overreach and overgrowth data, respectively. The final models (electronic supplementary material, tables S2 and S3) explained variability in coral competitive performances at 66.6% in terms of net overreach and 79.0% in terms of net overgrowth (electronic supplementary material, figures S3 and S4). This is relatively high compared to previous attempts (e.g. [23,24,32]) and considering the many additional biological and environmental factors that may influence competitive outcome between two living organisms (genotype, age, health, metabolic state, disturbance history, etc.), suggesting that our models accounted for key ecological gradients influencing coral competitive performances in our study system. Restricting data to the most abundant taxa resulted in similar patterns (electronic supplementary material, figures S5 and S6), confirming the prevalence of the identified mechanisms among dominant species.

A total of 1073 competitive interactions were recorded encompassing 41 taxa and eight morphotypes (electronic supplementary material, table S1) [35]. All surveys were performed by the same observer using SCUBA, occasionally assisted by another diver. Analyses and graphing were coded in R statistical software complemented by the mgcv package [45] (electronic supplementary material, appendix S2). Over-dispersed variables were log-transformed, and model diagnostics were performed by checking the assumptions of residual normality and homoscedasticity. Data were collected using non-invasive measurements on coral reef communities. The study was performed as part of the French National Institute of Research for Development's research activities on coral reef ecosystems of New Caledonia. No specific permits were required.

3. Results and discussion

3.1. Identifying drivers of coral competitive performance

Of the 1073 coral competitive interactions inspected, 84.3% (905) involved traces of tentacle deployment along the frontline, of which 7.4% (67, or 6.2% of all interactions) were bilateral. In 8.9% (6) of these bilateral overreach attacks, net space intrusions were tied between competitors (i.e. net overreach = 0). Similarly, 69.8% (749) of all interactions involved overgrowth, out of which 2.0% (15, or 1.4% of all interactions) were bilateral. In 13.3% (2) of these bilateral overgrowth attacks, net space invasions were tied between competitors (i.e. net overgrowth = 0). Only 0.5% (5) of all interactions were characterized as standoffs for both overgrowth and overreach, demonstrating the complementary nature of these two metrics to assess competitive wars among corals.

Coral competitive performances varied with attributes relative to individuals, interactions and environments, highlighting the interactive importance of biological and environmental factors in defining competitive outcomes. Overgrowth and overreach performances were both contingent on taxonomic identity, morphology, size, competitor abundance and shelf-position, whereas perimeter of contact and height differences only influenced overgrowth, and day of year only influenced overreach (electronic supplementary material, tables S2 and S3). As a metric of short-term competitive interactions, overreach reflects recently deployed battle strategies such as spontaneous attack-tentacle developments into opponent territories, brief skirmishes along the frontline that were seasonally variable in several taxa (figure 2c) and may reveal transitory in long-running competitive battles [22,25,30,32,34]. By contrast, as a more integrated measure of competitive interactions over time, overgrowth accounts for additional ecological mechanisms that prevail across successive battles in war strategy. This includes the capacity to sustain siege and lead large battlefields, sometimes for long times and simultaneously on multiple fronts (figure 1), performances that rely heavily on resource provisions and differ across taxa.

3.2. Individual-level attributes

Coral overgrowth and overreach performances differed among taxa as expected for species exhibiting contrasting life-history traits, with differences in growth form and rate, in tentacle size and reach, etc. [23,34,43]. Yet, contrasting responses to ecological gradients provided deeper insights into distinct life-strategies as reflected by different patterns of competitive performance across life-stages, as well as contrasting susceptibilities to environmental variation as reflected by segregated environmental optima. Larger corals generally exhibited higher net overgrowth, though many taxa deviated from a common size-dependent pattern in overgrowth and overreach (figures 2a and 3a). While evidence of size-dependent variability in coral competitive performance is not new [25,26], our comparative study indicates maximum competitive capacities occur at different stages among species, suggesting differences in size-specific investments in competition. Some taxa showed higher overgrowth and overreach at small sizes, potentially in a strategy to secure enough space early on, until reaching a size-refuge that guarantees survival and investment in other demographic processes such as reproduction [28,33,44]. This was the case for Porites, in which competitive performances declined with colony size (−0.3 cm in net overreach and −1.5 cm in net overgrowth across the size-range), with an inflection point at a size of approximately 15 cm diameter (figures 2a and 3a). Other taxa performed better at intermediate or larger sizes, which corresponds with higher ability in allocating large energetic resources to competitive battles. A marked positive effect of colony size was detected in mean overreach of Merulina (+14 cm across the size-range), Montastrea (+12 cm) and the soft-coral Sarcophyton (+7 cm), as well as in mean overgrowth of Goniastrea (+11 cm), Hydnophora (+9 cm), Merulina (+10 cm) and the soft-coral Nephthea (+70 cm). Nephthea is a particularly fierce competitor of reef-building corals with an unmatched ability to overgrow them (figure 3a) [21].

3.3. Interaction-level attributes

Coral competitive outcomes were influenced by several characteristics of species interactions, namely competitor abundance (a.k.a. number of enemies), contact perimeter (a.k.a. battlefield stretch) and height difference among competitors (equivalent to uneven battlegrounds). Competitor abundance was associated with changes in overreach performances of four coral taxa (figure 2b) and generally
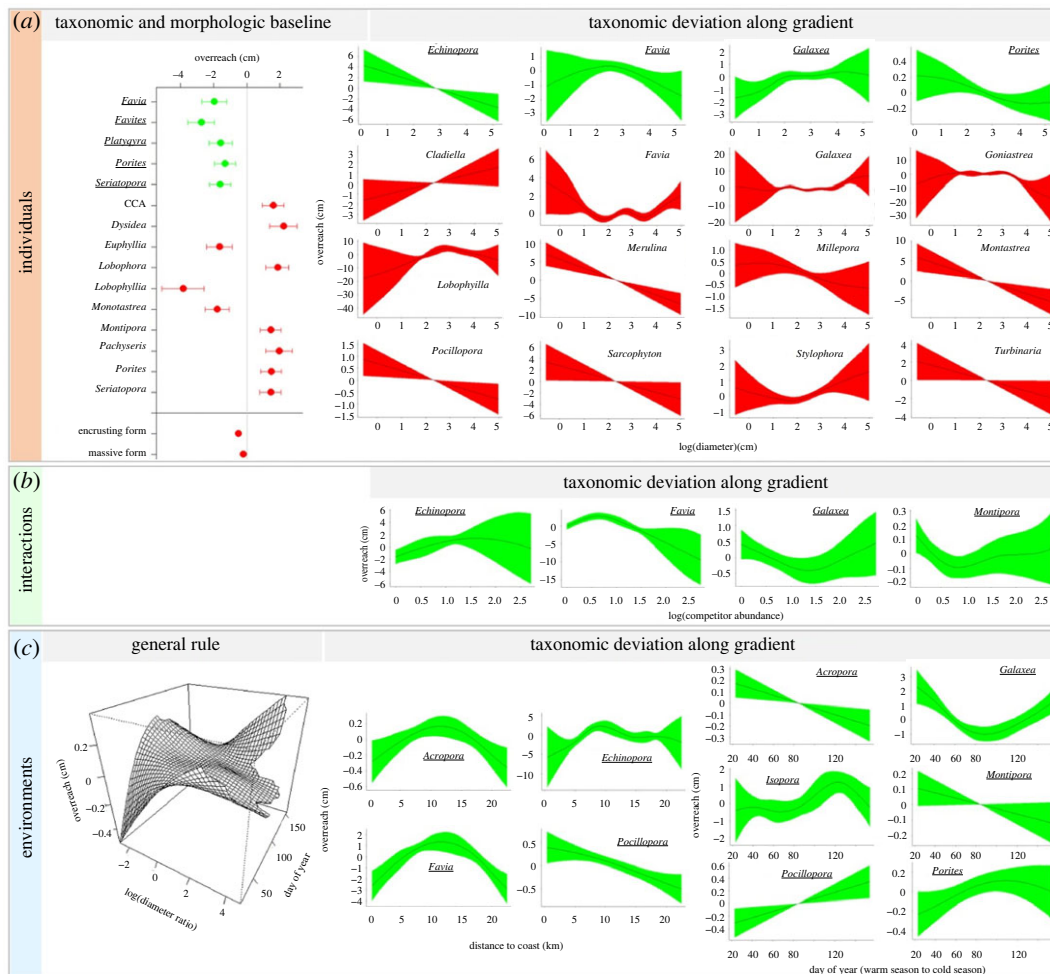
Figure 2. Changes in coral competitive performance as measured by net overreach distance along multiple ecological gradients, encompassing the effects of features associated with coral individuals (e.g. diameter), interactions (e.g. competitor abundance) and environments (e.g. distance to the coast). Plots illustrate partial contributions of different covariables to variation in net overreach of focal corals (mean ± s.e.). Each covariable accounts for an isolated portion of the variability in coral response, the overall coral competitive outcome being the result of the simultaneous effects of all covariables at the time. The covariables are organized by scale, characterizing which organisms are involved ((a), individuals), and how ((b), interactions) and where/when ((c), environments) the interactions occur. Covariables measured on focal corals are displayed in green with underlined species names (e.g. a negative effect of focal coral diameter on focal coral performance is observed for *Echinopora* in (a)). Covariables measured on competing organisms are displayed in red without underlined species names (e.g. a positive effect of competitor diameter on focal coral performance when competing with *Cladiella* is observed in (a)). Taxonomic and morphologic baselines identify differences in performance among species and growth forms once the effects of other ecological gradients are accounted for. Three-dimensional plot illustrates the interactive effects of two ecological gradients (covariate interaction) on the response of all species (i.e. general rule), while other plots indicate deviations specific to some taxa (covariate–factor interaction). Note differences in axes ranges. Texts in grey distinguish non-hard-coral species (CCA for crustose coralline algae). Only significant effects are illustrated (electronic supplementary material, table S2).

influenced size-specific overgrowth, with larger corals showing higher capacities in leading multi-front wars (figure 3b). Larger battlefields were associated with higher overgrowth in some taxa, such as *Millepora* and *Montipora* (+2 cm in net overgrowth), showing high capacities in waging large-scale competitive endeavours to the detriment of others such as *Porites*, in which a threshold in the capacity to hold space against competitors was observed (−10 cm in net overgrowth, with again a size-threshold at approximately 15 cm diameter, figure 3b). Overall, extended battlefield perimeters were associated with higher overgrowth performance in encrusting and columnar species and decreasing in branching and massive taxa, reflecting evolutionary differences in competitive abilities among morphological groups [24,43].
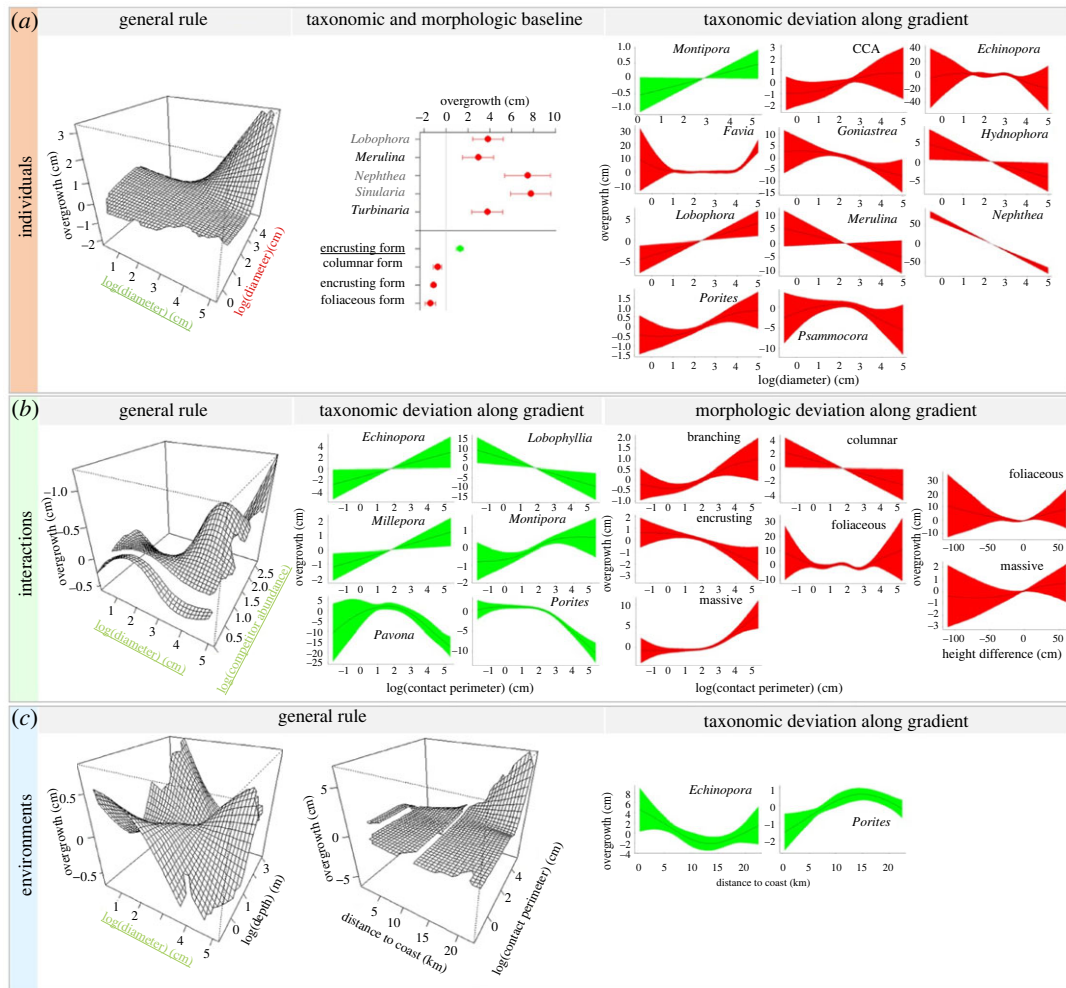
Figure 3. Changes in coral competitive performance as measured by net overgrowth distance along multiple ecological gradients, encompassing the effects of features associated with coral individuals (e.g. diameter), interactions (e.g. competitor abundance) and environments (e.g. distance to the coast). Plots illustrate partial contributions of different covariables to variation in net overgrowth of focal corals (mean ± s.e.). Each covariable accounts for an isolated portion of the variability in coral response, the overall coral competitive outcome being the result of the simultaneous effects of all covariables at the time. The covariables are organized by scale, characterizing which organisms are involved ((a), individuals), and how ((b), interactions) and where/when ((c), environments) the interactions occur. Covariables measured on focal corals are displayed in green with underlined species names (e.g. a positive effect of focal coral diameter on focal coral performance is observed for *Montipora* in (a)). Covariables measured on competing organisms are displayed in red without underlined species names (e.g. a positive effect of competitor diameter on focal coral performance when competing with CCA is observed in (a)). Taxonomic and morphologic baselines identify differences in performance among species and growth forms once the effects of other ecological gradients are accounted for. Three-dimensional plots illustrate the interactive effects of two ecological gradients (covariate interaction) on the response of all species (i.e. general rule), while other plots indicate deviations specific to some taxa and growth forms (covariate–factor interaction). Note differences in axes ranges. Texts in grey distinguish non-hard-coral species (CCA for crustose coralline algae). Only significant effects are illustrated (electronic supplementary material, table S3).

3.4. Environmental attributes

Battlefield environments also influenced coral competitive performances as reflected by the effects of shelf-position, depth and time, revealing differing environmental preferences among taxa (electronic supplementary material, tables S2 and S3). Cross-shelf variability in coral performances was detected in five taxa, among which peak overgrowth and/or overreach performances were spatially segregated. *Pocillopora* showed higher net overreach (+1 cm) near the coast compared to reefs situated further away, whereas *Acropora* (+0.6 cm) and *Favia* (+4 cm) peaked in mid-lagoon, *Porites* exhibited highest overgrowth (+2.0 cm) towards the barrier reef, and *Echinopora* showed contrasting spatial patterns

between overgrowth and overreach metrics (figures 2*c* and 3*c*). Similarly, net overreach performances varied seasonally in six taxa with a marked temporal segregation (figure 2*c*). *Acropora* (+0.4 cm) and *Montipora* (+0.2 cm) showed higher performance in the warm season, *Pocillopora* (+0.7 cm) in the cool season, *Isopora* (+1.5 cm) and *Porites* (+0.3 cm) during the inter-season, whereas *Galaxea* (+3.5 cm) peaked in each season. While the spatial differences in competitive performances among taxa confirm contrasting environmental optima along the coast-to-ocean gradient, the temporal patterns identified may reflect differences in environmental preferences *per se* (e.g. differing temperature optima) or different timings of investments in other demographic processes such as growth and reproduction (i.e. differing temporal windows). Indeed, territorial wars as well as growth and reproduction are energetically costly processes, and some corals may show temporal trade-offs in their investment in these endeavours [22,26,28,32]. For example, in New Caledonia as in the neighbouring Great Barrier Reef, acroporids including *Acropora* and *Montipora* reproduce at the onset of the warm season following a six-month period of gametogenesis, whereas other species such as *Pocillopora* reproduce throughout the year [48–51]. In addition, portions of the temporal trends identified may be attributable to response to external stimuli, which may explain the higher overreach observed in *Porites* during the inter-season between the performance peaks of acroporids and *Pocillopora*, and conversely high overreach in *Galaxea* during both seasons potentially as retaliation to attacks from these dominant taxa [32,37]. No taxonomic differences in coral performances across depth were detected (i.e. the non-significant term *Depth × Coral-taxon* was not retained in the models), although the size-dependent overgrowth response of corals generally varied with depth (electronic supplementary material, table S3; figure 3*c*).

3.5. Species baseline attributes

When the effects of ecological gradients were isolated (i.e. once accounting for the effects of the different covariables), species with encrusting and massive morphologies were associated with higher overreach (figure 2*a*), whereas encrusting, columnar and foliaceous species exhibited higher overgrowth (figure 3*a*). These differences may reflect differing evolutionary pathways among species. In contrast with other growth forms that enable escape via vertical growth, encrusting species are fully exposed to competition and their survival relies fundamentally on their capacity to preempt space on a two-dimensional substrate [14,22,33]. Similarly, several coral species with massive growth forms exhibit large polyps able to rebuff competitors on longer distances by developing long-range tentacles (figure 1) [20,23,24,34]. A maximum overreach distance of 5.7 cm performed by a massive *Galaxea* on a branching *Pocillopora* was recorded in this study, and the three massive taxa *Euphyllia*, *Lobophyllia* and *Montastrea* exhibited high baseline overreach (figure 2*a*). Noticeably, marked negative effects of competitors on coral overreach and overgrowth were only detected from hard- and soft-corals, whereas interactions with ascidians, sponges and algae were characterized solely by positive deviations from the average patterns (figures 2a and 3a). This suggests a less substantial effect of chemical wars alone as employed by these later taxa, compared to additional uses of physical wars involving tentacle-attacks as deployed by cnidarians, in direct competitive interactions [27,52,53].

3.6. Comprehending coral competitive interactions

Our study shows that coral competitive performances are governed by a complex interplay between who is involved and how, where and when the interactions occur, with outcomes in terms of net overreach and overgrowth that are largely predictable (figures 2 and 3). Species baseline performances associated with inherited taxonomic traits (e.g. tentacle reach) are modulated by a set of ecological gradients related to intrinsic characteristics of organisms (e.g. size and evolutionary life-strategy) as well as extrinsic features of their interactions and environments that vary in time and space (e.g. competitor abundance, contact perimeter and seasonality). The mechanisms governing coral competitive performances are therefore fundamentally analogous to those prevailing in human warfare where concerted military power (weapon abundance, deadliness and reach), war strategy (attack, defense and skirmish tactics), battle characteristics (stretch of battlefronts, duration of conflicts, number of enemies and allies), and battlefield features (battleground evenness and weather conditions) influence outcomes [54,55]. Notorious instances when battle characteristics and environmental condition influenced war outcome and sealed the fate of human history include the deleterious effects of multi-front wars for Napoleon's endeavour to expand the French empire across Europe between 1805 and 1815 [56], and the contribution of wintery weather conditions to Hitler's
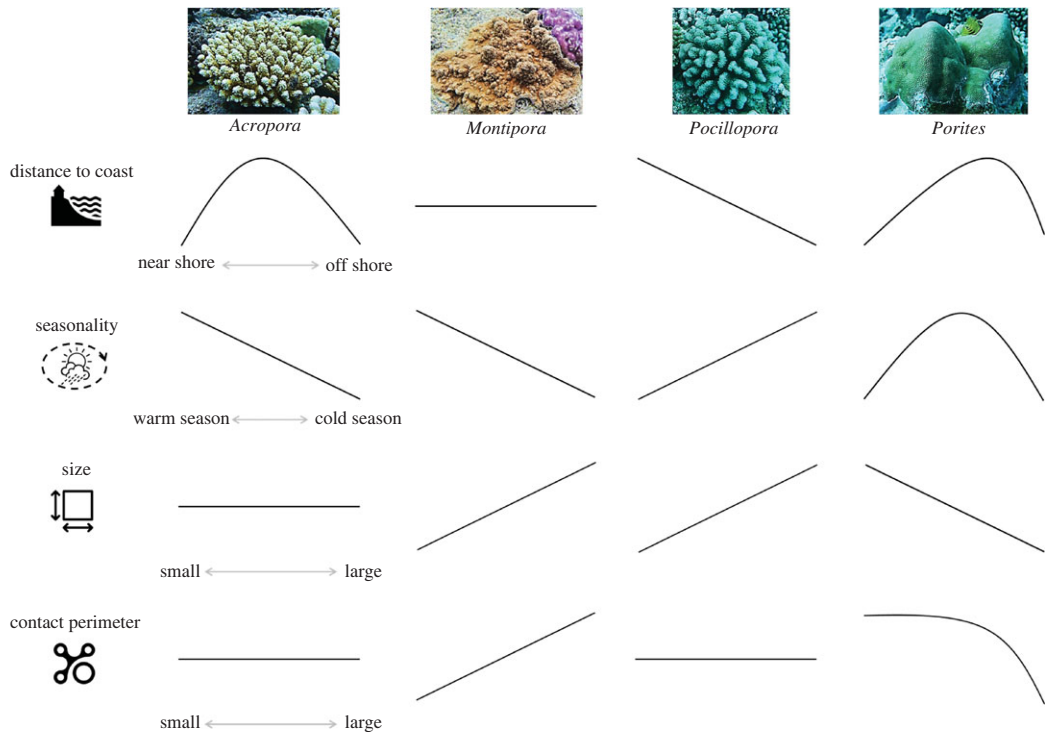
Figure 4. Multi-dimensional niche segregation among the four major reef-building coral taxa as revealed by variability in their competitive performances. The response patterns (summarized from figures 2 and 3) indicate segregation in time and space (different environmental preferences) as well as in life-strategies (different optimal sizes and warfare capacities).

army's defeat at the Soviet frontline in 1941 [57]. Another historical example relates to the Battle of Agincourt in 1415, a turn in the Hundred Years' War for the dominion of France and England, where muddy terrain following rainfall severely handicapped the heavily armoured knights of the numerically superior French army to the advantage of Henry V [58]. Similarly, in our study system, coral size (analogous to military size) and contact perimeter (analogous to battlefield stretch) were negatively associated with warfare performances of *Porites* in contrast with *Montipora* for whom the effects were positive, and summer conditions favoured *Acropora* with a contrary effect for *Pocillopora* (figure 4). In human history as well as in ecological science, understanding such regulatory mechanisms is key to comprehending past events and anticipating future outcomes.

3.7. Niche segregations and implications in changing environments

The contrasted responses of coral taxa as identified across multiple ecological gradients provide new insights into the variety of mechanisms underlying niche segregation in biodiverse species assemblages. Indeed, the diversity of ecological windows occupied by species is reflected in the contrasting environmental preferences revealed by differing performances in time and space, as well as the divergent evolutionary pathways as indicated by different responses to individual- and interaction-level attributes (figure 4). These differences may explain how the species coexist as a result of distinct demographic life-strategies, environmental heterogeneity and competitive interactions, resulting in the exceptional biodiversity observed on reefs [17,23,28,43]. Nevertheless, several key coral taxa were sensitive to environmental variability as reflected by distance to the coast and seasonality, indicating that their competitive success, and perhaps overall fitness, may be affected by alterations of coastal environments. Our findings suggest that warmer oceanic conditions, similar to those presently observed in summer, may advantage higher competitive performances of acroporids to the detriment of pocilloporids, although further anthropization of coastal habitats, resulting in altered water quality and ecological communities as currently found near the coastline [38–41], benefits pocilloporids over acroporids (figure 4). In New Caledonia and globally, acroporids contribute exceptionally to coral reef structural complexity, biodiversity and calcification [13,37,59–61]. Despite high capabilities to dominate reefs in peri-optimal environments, acroporids are particularly sensitive to environmental stressors such as warming and declining water quality, with community shifts from acroporid dominance to

pocilloporids or poritids often observed in sub-optimal conditions [7,10,11,29,42]. Widespread acroporid declines have been associated with reef environment degradation in various regions including the Caribbean, Persian Gulf, Great Barrier Reef and French Polynesia [12,15,16,62]. In contrast with other regions where acroporids appear to face their upper temperature limits [11,29], our study suggests acroporid performances may actually increase in a warmer climate in the sub-tropical reef system of New Caledonia where few large-scale episodes of coral bleaching have yet been recorded. Nevertheless, restraining anthropization of coastal environments, notably pollution and fishing stress, appears key to preserving near shore acroporid populations and their unique contributions to reef accretion and resilience.

4. Conclusion

As global changes increasingly alter coastal marine environments, some ecosystems are inexorably expected to collapse while others may transform to new community compositions, structures and functions, changes that remain hard to predict [1,3,4,11]. Nevertheless, present trajectories of coastal degradation indicate future coral reef environments may increasingly resemble those found near dense human concentrations today [6–8]. Our study suggests that such anthropization results in lower abilities of some major coral taxa in preempting reef space via direct competition. Because corals are slow-growing habitat-forming species at the basis of reef ecosystems, such differences in competitive performances may result in extirpations of vulnerable populations, with implications for reef ecosystem biodiversity and services to society.

Overall, competitive performance appears as an effective, widespread and accessible indicator of species performances across various ecological gradients. As a measure of species' abilities in such a costly and vital process as defending and extending their living space, it can serve as a proxy of species health, fitness and therefore ecological success. As in our coral reef study system, differences in competitive performance can help identify the biological and environmental constraints underlying ecological niches and environmental windows that define species distributions, coexistence and therefore biodiversity patterns. Given the many ecological pathways that link species' performances to their environment, we encourage similar quantitative investigations to further understanding of determinants of species interactions at the interplay between evolutionary traits, life-strategies and global changes, and implications for the dynamics of ecosystems in a changing environment.

References

1. Jouffray JB, Blasiak R, Norström AV, Österblom H, Nyström M. 2020 The Blue Acceleration: the trajectory of human expansion into the ocean. *One Earth* **2**, 43–54. (doi:10.1016/j.oneear.2019. 12.016)

2. Carturan BS, Pither J, Maréchal JP, Bradshaw CJ, Parrott L. 2020 Combining agent-based, trait-based and demographic approaches to model coral-community dynamics. *Elife* **9**, e55993. (doi:10.7554/eLife.55993)

3. WWF. 2020 Living planet report 2020. In *Bending the curve of biodiversity loss* (eds REA Almond, M Grooten, T Petersen). Gland, Switzerland: WWF. See https://livingplanet.panda.org.

4. Díaz S *et al.* 2020 Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. *Zenodo* (doi:10.5281/zenodo. 3553579)

5. Kayal M, Lewis H, Ballard J, Kayal E. 2019 Humanity and the 21st century's resource gauntlet: a commentary on Ripple *et al.*'s article 'World scientists' warning to humanity: a second notice'. *Rethinking Ecol.* **4**, 21–30. (doi:10.3897/rethinkingecology.4.32116)

6. Cinner JE *et al.* 2020 Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science* **368**, 307–311. (doi:10.1126/science.aax9412)

7. Darling ES *et al.* 2019 Social-environmental drivers inform strategic management of coral reefs in the Anthropocene. *Nat. Ecol. Evol.* **3**, 1341–1350. (doi:10.1038/s41559-019-0953-8)

8. Duprey NN *et al.* 2020 Megacity development and the demise of coastal coral communities: evidence from coral skeleton δ^{15}N records in the Pearl River estuary. *Glob. Change Biol.* **26**, 1338–1353. (doi:10.1111/gcb.14923)

9. Souter D, Planes S, Wicquart J, Logan M, Obura D, Staub F. 2021. *Status of Coral Reefs of the World: 2020.* Townsville, Australia: ICRI, GCRMN, Australia Institute of Marine Science, UNEP. (www.unep.org/resources/status-coral-reefs-world-2020)

10. Adjeroud M, Kayal M, Iborra-Cantonnet C, Vercelloni J, Bosserelle P, Liao V, Chancerelle Y, Claudet J, Penin L. 2018 Recovery of coral assemblages despite acute and recurrent disturbances on a South Central Pacific reef. *Sci. Rep.* **8**, 1–8. (doi:10.1038/s41598-018-27891-3)

11. Hughes TP *et al.* 2018 Global warming transforms coral reef assemblages. *Nature* **556**, 492–496. (doi:10.1038/s41586-018-0041-2)

12. Cramer KL, Jackson JB, Donovan MK, Greenstein BJ, Korpanty CA, Cook GM, Pandolfi JM. 2020 Widespread loss of Caribbean acroporid corals was underway before coral bleaching and disease outbreaks. *Sci. Adv.* **6**, eaax9395. (doi:10.1126/sciadv.aax9395)

13. Carlot J *et al.* 2021 Juvenile corals underpin coral reef carbonate production after disturbance. *Glob. Change Biol.* **27**, 2623–2632. (doi:10.1111/gcb.15610)

14. Wakeford M, Done TJ, Johnson CR. 2008 Decadal trends in a coral community and evidence of changed disturbance regime. *Coral Reefs* **27**, 1–13. (doi:10.1007/s00338-007-0284-0)

15. Kayal M, Lenihan HS, Brooks AJ, Holbrook SJ, Schmitt RJ, Kendall BE. 2018 Predicting coral community recovery using multi-species population dynamics models. *Ecol. Lett.* **21**, 1790–1799. (doi:10.1111/ele.13153)

16. Riegl B, Johnston M, Purkis S, Howells E, Burt J, Steiner SC, Sheppard CR, Bauman A. 2018 Population collapse dynamics in *Acropora downingi*, an Arabian/Persian Gulf ecosystem-engineering coral, linked to rising temperature. *Glob. Change Biol.* **24**, 2447–2462. (doi:10.1111/gcb.14114)

17. Connell JH. 1978 Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310. (doi:10.1126/science.199.4335.1302)

18. Menge BA, Sutherland JP. 1987 Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* **130**, 730–757. (doi:10.1086/284741)

19. Mumby PJ, Hastings A, Edwards HJ. 2007 Thresholds and the resilience of Caribbean coral reefs. *Nature* **450**, 98–101. (doi:10.1038/nature06252)

20. Sheppard CRC. 1979 Interspecific aggression between reef corals with reference to their distribution. *Mar. Ecol. Prog. Ser.* **1**, 237–247. (doi:10.3354/meps001237)

21. Sammarco PW, Coll JC, La Barre S. 1985 Competitive strategies of soft corals (Coelenterata: Octocorallia). II. Variable defensive responses and susceptibility to scleractinian corals. *J. Exp. Mar. Biol. Ecol.* **91**, 199–215. (doi:10.1016/0022-0981(85)90176-5)

22. Romano SL. 1990 Long-term effects of interspecific aggression on growth of the reef-building corals *Cyphastrea ocellina* (Dana) and *Pocillopora damicornis* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* **140**, 135–146. (doi:10.1016/0022-0981(90)90087-S)

23. Precoda K, Allen AP, Grant L, Madin JS. 2017 Using traits to assess nontransitivity of interactions among coral species. *Am. Nat.* **190**, 420–429. (doi:10.1086/692758)

24. Alvarez-Noriega M, Baird AH, Dornelas M, Madin JS, Connolly SR. 2018 Negligible effect of competition on coral colony growth. *Ecology* **99**, 1347–1356. (doi:10.1002/ecy.2222)

25. Russ GR. 1982 Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia* **53**, 12–19. (doi:10.1007/BF00377130)

26. Rinkevich B, Loya Y. 1983 Intraspecific competitive networks in the Red Sea coral *Stylophora pistillata*. *Coral Reefs* **1**, 161–172. (doi:10.1007/BF00571193)

27. Porter JW, Targett NM. 1988 Allelochemical interactions between sponges and corals. *Biol. Bull.* **175**, 230–239. (doi:10.2307/1541563)

28. Kayal M, Vercelloni J, Wand MP, Adjeroud M. 2015 Searching for the best bet in life-strategy: a quantitative approach to individual performance and population dynamics in reef-building corals. *Ecol. Complexity* **23**, 73–84. (doi:10.1016/j.ecocom.2015.07.003)

29. Samiei JV, Saleh A, Mehdinia A, Shirvani A, Kayal M. 2015 Photosynthetic response of Persian Gulf acroporid corals to summer versus winter temperature deviations. *PeerJ* **3**, e1062. (doi:10.7717/peerj.1062)

30. Logan A. 1984 Interspecific aggression in hermatypic corals from Bermuda. *Coral Reefs* **3**, 131–138. (doi:10.1007/BF00301957)

31. Sheppard CRC. 1985 Unoccupied substrate in the central Great Barrier Reef: role of coral interactions. *Mar. Ecol. Prog. Ser.* **25**, 259–268. (doi:10.3354/meps025259)

32. Chornesky EA. 1989 Repeated reversals during spatial competition between corals. *Ecology* **70**, 843–855. (doi:10.2307/1941353)

33. Barott KL, Williams GJ, Vermeij MJ, 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. *Mar. Ecol. Prog. Ser.* **460**, 1–12. (doi:10.3354/meps09874)

34. Ferriz-Domínguez N, Horta-Puga G. 2001 Short-term aggressive behavior in scleractinian corals from La Blanquilla reef, Veracruz Reef System. *Revista de Biología Trop.* **49**, 67–75.

35. Kayal M, Adjeroud M. 2022 Data from: the war of corals: patterns, drivers, and implications of changing coral competitive performances across reef environments. Dryad Digital Repository. (doi:10.5061/dryad.98sf7m0kn)

36. Andréfouët S, Torres-Pulliza D. 2004 *Atlas des récifs coralliens de Nouvelle-Calédonie.* Nouméa, France: IFRECOR Nouvelle-Calédonie, IRD. See www.documentation.ird.fr/hor/fdi:010045824.

37. Adjeroud M, Poisson E, Peignon C, Penin L, Kayal M. 2019 Spatial patterns and short-term changes of coral assemblages along a cross-shelf gradient in the Southwestern Lagoon of New Caledonia. *Diversity* **11**, 21. (doi:10.3390/d11020021)

38. Jacquet S, Delesalle B, Torréton JP, Blanchot J. 2006 Response of phytoplankton communities to increased anthropogenic influences (southwestern lagoon, New Caledonia). *Mar. Ecol. Prog. Ser.* **320**, 65–78. (doi:10.3354/meps320065)

39. Fichez R, Chifflet S, Douillet P, Gérard P, Gutierrez F, Jouon A, Ouillon S, Grenz C. 2010 Biogeochemical typology and temporal variability of lagoon waters in a coral reef ecosystem subject to terrigeneous and anthropogenic inputs (New Caledonia). *Mar. Pollut. Bull.* **61**, 309–322. (doi:10.1016/j.marpolbul.2010.06.021)

40. Ouillon S *et al.* 2010 Circulation and suspended sediment transport in a coral reef lagoon: the south-west lagoon of New Caledonia. *Mar. Pollut. Bull.* **61**, 269–296. (doi:10.1016/j.marpolbul.2010.06.023)

41. Gonson C, Pelletier D, Alban F, Giraud-Carrier C, Ferraris J. 2017 Influence of settings management and protection status on recreational uses and pressures in marine protected areas. *J. Environ. Manage.* **200**, 170–185. (doi:10.1016/j.jenvman.2017.05.051)

42. Moustaka M, Mohring MB, Holmes T, Evans RD, Thomson D, Nutt C, Stoddart J, Wilson SK. 2019 Cross-shelf heterogeneity of coral assemblages in Northwest Australia. *Diversity* **11**, 15. (doi:10.3390/d11020015)

43. Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM. 2012 Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.* **15**, 1378–1386. (doi:10.1111/j.1461-0248.2012.01861.x)

44. Hall VR, Hughes TP. 1996 Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology* **77**, 950–963. (doi:10.2307/2265514)

45. Wood S. 2017 *Generalized additive models: an introduction with R.* Boca Raton, FL: CRC press.

46. Ruppert D, Wand MP, Carroll RJ. 2003 *Semiparametric regression.* Cambridge, UK: Cambridge University Press.

47. Akaike H. 1978 A Bayesian analysis of the minimum AIC procedure. *Ann. Instit. Stat. Math.* **30**, 9–14. (doi:10.1007/BF02480194)

48. Heyward AJ, Collins JD. 1985 Growth and sexual reproduction in the scleractinian coral *Montipora digitata* (Dana). *Mar. Freshw. Res.* **36**, 441–446. (doi:10.1071/MF9850441)

49. Baird AH, Kospartov MC, Purcell S. 2010 Reproductive synchrony in *Acropora* assemblages on reefs of New Caledonia. *Pacific Sci.* **64**, 405–412. (doi:10.2984/64.3.405)

50. Keith SA *et al.* 2016 Coral mass spawning predicted by rapid seasonal rise in ocean temperature. *Proc. R. Soc. B* **283**, 20160011. (doi:10.1098/rspb.2016.0011)

51. Smith HA, Moya A, Cantin NE, van Oppen MJ, Torda G. 2019 Observations of simultaneous sperm release and larval planulation suggest reproductive assurance in the coral *Pocillopora acuta*. *Front. Mar. Sci.* **6**, 362. (doi:10.3389/fmars.2019.00362)

52. Suchanek THD, Green J. 1981 *Interspecific competition between Palythoa caribaeorum and other sessile invertebrates on St. Croix reefs, US Virgin Islands*. In *Proc. of the 4th Int. Coral Reef Symp., Manila, Philippines, 18–22 May 1981*, pp. 679–684. Manila, Philippines: University of the Philippines.

53. Smith JE *et al*. 2006 Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecol. Lett.* **9**, 835–845. (doi:10.1111/j.1461-0248.2006.00937.x)

54. Tzu S, Tzu S, Sun W, Vu SC. 1971 *The art of war*, 216p. Oxford, UK: Oxford University Press.

55. Diamond J. 2005 *Collapse: how societies choose to fail or succeed*, 592p. London, UK: Penguin.

56. Roberts A. 2014 *Napoleon: a life*, 976p. London, UK: Penguin.

57. Burleigh M. 2000 *The third reich: a new history*, 965p. New York, NY: Hill and Wang.

58. Mortimer I. 2009 *1415: henry V's year of glory*, 640p. London, UK: Bodley Head.

59. Fenner D, Muir P. 2008 Reef corals of the northwestern lagoon of Grande-Terre, New Caledonia. In *A Rapid Marine Biodiversity Assessment of the Coral Reefs of the Northwest Lagoon, Between Koumac and Yandé, Province Nord, New Caledonia*. Conservation International, BioOne, 18–32. (doi:10.1896/054.053.0102)

60. Blanchon P, Granados-Corea M, Abbey E, Braga JC, Braithwaite C, Kennedy DM, Spencer T, Webster JM, Woodroffe CD. 2014 Postglacial fringing-reef to barrier-reef conversion on Tahiti links Darwin's reef types. *Sci. Rep.* **4**, 1–9. (doi:10.1038/srep04997)

61. Hongo C, Wirrmann D. 2015 Preliminary identification of key coral species from New Caledonia (Southwest Pacific Ocean), their significance to reef formation, and responses to environmental change. *Island Arc* **24**, 31–46. (doi:10.1111/iar.12090)

62. Clark TR, Roff G, Zhao JX, Feng YX, Done TJ, McCook LJ, Pandolfi JM. 2017 U-Th dating reveals regional-scale decline of branching *Acropora* corals on the Great Barrier Reef over the past century. *Proc. Natl Acad. Sci. USA* **114**, 10 350–10 355. (doi:10.1073/pnas.1705351114)

63. Kayal M, Adjeroud M. 2022 The war of corals: patterns, drivers, and implications of changing coral competitive performances across reef environments. FigShare. (doi:10.6084/m9.figshare.c.6026241)

64. Kayal M, Adjeroud M. 2021 The war of corals: patterns, drivers, and implications of changing coral competitive performances across reef environments. *bioRxiv*. (doi:10.1101/2021.12.06.471466)