

The global biogeography of reef morphology

Lucas L. Lutzenkirchen^{1,2}  | Stephanie J. Duce² | David R. Bellwood^{1,2} 

¹Research Hub for Coral Reef Ecosystem Functions, College of Science and Engineering, James Cook University, Townsville, Queensland, Australia

²College of Science and Engineering, James Cook University, Townsville, Queensland, Australia

Correspondence

Lucas L. Lutzenkirchen, Research Hub for Coral Reef Ecosystem Functions, College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia.

Email: lucas.lutzenkirchen@my.jcu.edu.au

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Abstract

Aim: The Caribbean and Indo-Pacific are separate biogeographical realms with distinct biogeographical and evolutionary histories, a 10-fold difference in biodiversity, and highly disparate sea-level histories. Since reef morphology often reflects interactions between biological activity and biogeographical history, including sea levels, the widths of shallow coral reef habitats are likely to differ markedly between realms, with ramifications for numerous ecosystem functions. Our goal, therefore, was to assess the impact of global-scale biogeographical and evolutionary histories on coral reef habitats. Specifically, are Indo-Pacific reefs wider than their Caribbean counterparts?

Location: Global.

Time Period: Modern.

Major Taxa Studied: Coral reefs.

Methods: We used the Allen Coral Atlas, a global reef mapping system (3 m pixel resolution), to examine 3765 transects, 3 km long and 1 km apart, on 60 reefs across the two realms, quantifying shallow reef habitat widths (Inner and Outer Reef Flat, and Reef Crest) using ArcGIS.

Results: Shallow reef habitat widths were strikingly similar between the Caribbean and Indo-Pacific. Estimated modal widths diverged by just 37 m; means by just 122 m. Although shallow reef zones appeared to be wider in the Indo-Pacific, habitat widths on atolls were almost identical across realms (means varying by less than 8 m).

Main Conclusions: Our remote sensing approach provides a global description of the biogeography of coral reefs as biogenic structures. Furthermore, we can assess the relative importance of realm-wide differences in coral diversity and sea-level history on reef growth. The striking similarity of reef widths across realms suggests that reef growth (net reef accretion) is largely independent of coral diversity, or sea-level history, and that other factors may have played a major role in constraining shallow reef widths. These factors may include geomorphology (e.g. antecedent topography and historical accommodation space) and, once at sea level, self-limiting local hydrodynamics.

KEYWORDS

Allen Coral Atlas, biogeography, Caribbean reefs, coral reefs, evolutionary history, Indo-Pacific reefs, reef morphology, remote sensing

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1 | INTRODUCTION

Coral reef ecosystems are exceptional in their ability to create broad-scale (10 s–100 s of km) biogenic structures and their own substratum. Coral reefs represent the ultimate expression of an interaction between the biology of organisms and their environment (Smith & Buddemeier, 1992). Their morphology and configuration, including shape and size, reflect the relationship between biological activity and biogeographical history, as well as physical hydrodynamic drivers. While coral reefs are incredibly diverse systems globally, they share basic, fundamental, habitat structures and zonation patterns (Goreau et al., 1979). Thus, all coral reefs can be broadly divided into distinct omnipresent habitat zones, including the reef slope, crest, and flat, each with its own distinct community composition and structure (Bellwood et al., 2018; Chappell, 1980; Done, 1983; Goreau, 1959; Stoddart, 1969). The relative size of these habitat zones can vary, and this variation can help to characterize different coral reef systems around the globe (Adey, 1978; Done, 1983; Dullo, 2005).

Reef flats are arguably the most conspicuous of all shallow water reef zones (Bellwood et al., 2018; Yamano et al., 2001). They are defined by coral reef growth having reached modern sea level (Thornborough & Davies, 2011) and are often the largest zone of a coral reef by area (Bellwood et al., 2018). Due to their shallow nature, reef flats are highly variable but productive habitats (Bellwood et al., 2018; Hatcher, 1988) and are also important dissipators of wave energy (Harris et al., 2015; Kench & Brander, 2006). Thus, the extent (i.e. width) of reef flats is an important proxy for reef productivity and coastal buffering. Assessing the global distribution of reef widths may also have implications for understanding how reefs, as broadscale biogenic structures, form and evolve over time and which factors are most important in determining their growth.

The Caribbean and Indo-Pacific are highly divergent biogeographical realms in terms of their evolutionary history, biogeography, and biodiversity (Bellwood et al., 2017; Cowman & Bellwood, 2013a;

Siqueira et al., 2019a) (Figure 1a). They also differ markedly in their sea-level history and timing of reef initiation (Gischler, 2010, 2015; Montaggioni & Braithwaite, 2009; Woodroffe & Webster, 2014) (Figure 1b).

Geologically, the long-term biogeographical and evolutionary differences between the Caribbean and the Indo-Pacific coincide with more recent disparities in sea-level history (Figure 1b). The Holocene period (ca. 11,500 YBP–present), for example, has been characterized by widespread environmental change, including extensive global sea-level rise (Bard et al., 1996; Fairbanks, 1989). In the Caribbean, sea-level history can be described by a transgressive curve, where sea levels rose rapidly during the Mid-Holocene, but decelerated afterwards, never exceeding modern sea levels (Gischler, 2015). By contrast, in the Indo-Pacific, after a steep initial rise, reef systems experienced relatively static sea levels (1–2 m above modern levels) for the past 6000 years, with a fall towards modern levels at the end of the Holocene (Gischler, 2010) (Figure 1b).

Sea level is a major controlling factor, determining both the onset of coral reef growth and the lateral extent of shallow reef zones. This control is manifested through its impact on available vertical accommodation space (Kennedy & Woodroffe, 2002), which is a function of sea-level changes and antecedent (basement) topography (Camoin & Webster, 2015; Gischler, 2015). Reefs are thus commonly categorized as 'keep-up', 'catch-up' or 'give up' according to their response to sea-level rises increasing the available accommodation space (Davies & Montaggioni, 1985; Neumann & Macintyre, 1985).

Given that Indo-Pacific reefs had sea levels at or above present for approximately 6 ka longer than Caribbean reefs they have had considerably more time to accrete laterally regardless of whether they were 'keep-up' or 'catch-up' reefs. A review of Indo-Pacific reefs found lateral accretion rates ranged from 8 to 330 m/ka with a mean of 84 m/ka (Yamano et al., 2003). Given these rates, one may expect Indo-Pacific shallow reef habitats to be about 500 m wider than their Caribbean counterparts. This sustained growth could be expected to be further facilitated by the higher diversity of corals in the Indo-Pacific.

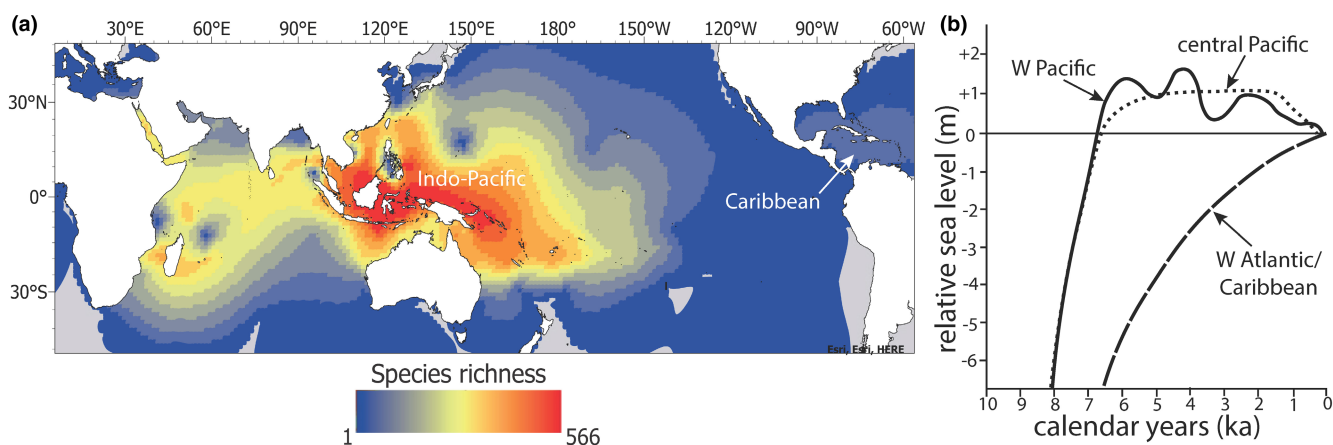


FIGURE 1 (a) Coral species richness across the tropics of the world (Ecoregions based on Spalding et al., 2007 and coral species richness data: www.coralsoftheworld.org, see Veron et al., 2015), (b) Holocene relative sea-level curves for the Western Atlantic/Caribbean and Pacific (from Gischler, 2010, modified).

The highly disparate coral species richness and composition of Caribbean and Indo-Pacific reefs was primarily driven by tectonic activity during the Miocene, which resulted in the formation of hard geological barriers that isolated the Atlantic and Caribbean from the Indo-Pacific (Cowman & Bellwood, 2013b; Lessios, 2008; O'Dea et al., 2007) and by intensifying extinctions of coral lineages in the Caribbean during the Plio-Pleistocene (Budd et al., 2011; van Woesik et al., 2012). Coral reefs in the Caribbean (Tropical Western Atlantic) show a much more depauperate coral and fish fauna, compared to reefs in the Indo-Pacific (Bellwood et al., 2004; Cowman & Bellwood, 2013b; Siqueira et al., 2019b; Spalding et al., 2001) (Figure 1a). Coral species richness in the Indo-Pacific is an order of magnitude higher than in the Caribbean (the Caribbean has just 51 coral species compared to almost 700 in the Indo-Pacific; Roff, 2021). Furthermore, many coral lineages in the Atlantic (including most Caribbean species) are evolutionary distinct (Fukami et al., 2004), emphasizing a long evolutionary history driven by isolation (Bellwood & Wainwright, 2002; Floeter et al., 2008). If coral biodiversity promotes reef growth, or ecosystem resilience or stability, one may therefore expect greater and/or more sustained growth of reefs in the Indo-Pacific.

The impact of these potential drivers of regional reef development may have significant implications for reef habitat widths, the functionality of shallow reef systems and their response to climate change. As some of the most productive reef habitats (Bellwood et al., 2018; Kench et al., 2022), with a major influence on wave attenuation (Harris et al., 2015), and sediment retention (Schlaefter et al., 2022), any differences in reef habitat widths could have far-reaching implications for the sustainability of reefs and their future ability to deliver ecosystem services to humans (Morais et al., 2021; Tebbett et al., 2022). Thus, globally, reefs may differ markedly in their ability to deliver key functions. However, there has been no quantification of global differences in the widths of shallow reef habitats.

Historically, the spatial quantification of reefs has been restricted by the available data. However, advances in remote sensing now permit the assessment of reefs at global scales and in increasingly high detail (Hedley et al., 2016; Kutser et al., 2020). The Allen Coral Atlas enables us to undertake the first standardized worldwide assessment of benthic cover and geomorphic zonation of coral reefs using fine-scale (3 m) resolution imagery and maps (Allen Coral Atlas, 2022). This study utilizes this cutting-edge dataset to investigate how the contrasting biogeographical and regional evolutionary histories of the Caribbean and Indo-Pacific may have shaped shallow reef width patterns at 60 reefs in 20 locations within these two realms. Specifically, transects spaced at 1 km intervals were used to (1) quantify shallow reef habitat widths between the Caribbean and Indo-Pacific and (2) explore potential geological, ecological and biogeographical drivers of any differences. The key question is: Are Indo-Pacific shallow reef habitats broader than their Caribbean counterparts, and, if so, what are the potential implications for reefs given escalating climate change?

2 | METHODS

2.1 | Data acquisition

Biogeographical variation in the width of shallow coral reef ecosystems was evaluated using the Allen Coral Atlas, a global mapping project aiming to combine conventional ecological-biophysical perspectives of coral reef ecosystems with an earth observation systems view of reefs, provided through remote sensors (Kennedy et al., 2021). The Coral Allen Atlas uses PlanetScope (Dove) imagery (Allen Coral Atlas, 2022) and the 'Reef Cover' classification described by Kennedy et al. (2021), which combines machine-based learning algorithms and Object-Based-Analysis (Lyons et al., 2020) to create a coral reef classification system consisting of 17 geomorphic class descriptors. Our study used this new and freely available data resource to investigate the width of shallow water reef zones across 3765 transects on 60 reefs across the Indo-Pacific ($n=30$) and Caribbean ($n=30$) (Figure 2) (accessed: March 2022). Shallow water reef zones were defined as the inner flat, outer flat and reef crest zones of the Allen Coral Atlas' geomorphic map (accessed: March 2022). To facilitate between-realm comparisons, sample reefs were chosen to ensure a balanced sample in both realms based on reef types, individual reef area and location (oceanic vs continental) (see Supplementary Information Text S1 for further information). Major reef types were classified as Barrier reefs ($n=11$), Atolls ($n=10$), Low Islands ($n=2$) and High Islands (sensu Nunn et al., 2016) ($n=37$). In our analyses, we purposefully did not include reefs close to, or attached to, mainland shores that could be classified as 'fringing reefs'. The term is very broad and lacks consistent definition, as fringing reef types vary markedly on a global scale (Kennedy et al., 2021). Therefore, 'fringing reefs' were only included if located adjacent to isolated islands. In these cases, the topography of the adjacent island was used to differentiate such reef systems, following Nunn et al. (2016) (categorizing islands with elevations above 30 m as high islands). Furthermore, to minimize the potential for variation in terrestrial influences and coastal effects, including turbidity, compromising image classification accuracy, we excluded the 'Terrestrial Reef Flat' class (as defined by Kennedy et al., 2021) from our analyses. Our approach, as applied to both realms, therefore, focusses solely on shallow reef habitat width estimates from geomorphic zones (Inner Reef Flat, Outer Reef Flat and Reef Crest) that are interrelated in the classification scheme, widely supported in the geological and ecological literature, and in locations where terrestrial influences are likely to be limited or non-existent. Therefore, we specifically look at reefs in shallow, clear water situations. Outer reef flats are defined by the Allen Coral Atlas as shallow, strictly horizontal habitats, characterized by increased coral cover and relatively high wave energy gradients. Inner reef flats, on the other hand, are deeper, gently sloping habitats, dominated by the presence of sand-covered substrata. Reef crests are defined as the narrow zones experiencing the greatest wave exposure, dominated by hard-bottom substrata with little structural complexity

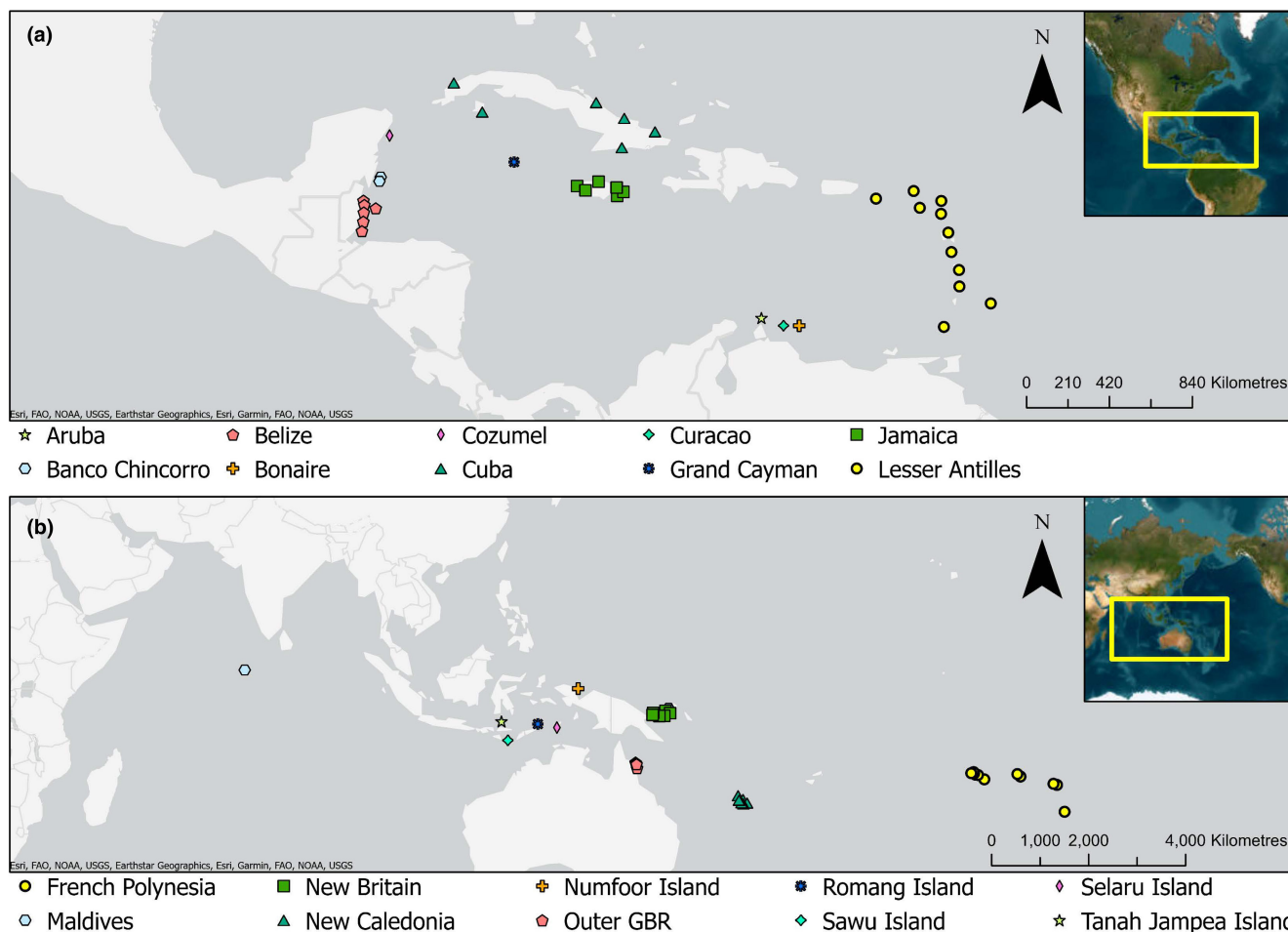


FIGURE 2 Map of the 20 reef locations and 60 reefs used in this study in the Caribbean (a) and Indo-Pacific (b).

(Kennedy et al., 2021). These classifications use interzonal relationships as part of their class description, meaning that Inner Reef Flat, Outer Reef Flat and Reef Crest must be adjacent to one another, and in that order, increasing accuracy within these class descriptors. Map accuracies partially depend on the availability of reference data, as well as potential obstructions that may vary across locations. The Supporting Information (Table S1) includes a comprehensive list of further potential limitations inherent to the mapping process. It must also be noted that while our data are based on the cumulative result of thousands of years of reef growth, the observations are only a present-day snapshot. We do not consider the timing of growth initiation beyond that implied by the regional profiles outlined above.

2.2 | Geospatial analysis

The geomorphic zones for the study reefs were downloaded from Allen Coral Atlas (Allen Coral Atlas, 2022). The desired reef zones (inner flat, outer flat and crest) were then selected (Figure 3b). A polyline was created along the outline of each reef, roughly following the crest (Figure 3c). Along this outline of each reef, 3-km long

cross-reef transects were generated every kilometre (Figure 3d). Reef width transects were also classified by exposure status, according to the prevailing wind in the region (e.g. leeward or windward) accessed through a simulated and modelled weather dataset created by meteoblue (Meteoblue, 2022). Modelled wind roses were used to identify the prevailing wind direction and to assign each transect to an exposure category (exposed, sheltered). Potential limitations and caveats of the dataset are described in Table S1 of the supplementary material. Finally, we measured the width of the reef zones intersected by each transect. All geospatial analyses were performed in the software ArcGIS Pro 2.7.0 (Esri Inc, 2022).

2.3 | Data exploration

Measurements of the inner flat, outer flat, and crest widths on each transect were summed to calculate the total shallow reef habitat width on that transect. Transects with a shallow reef width of 0 were excluded from further analysis. All statistical analyses were conducted in the software R (R Core Team, 2022), using 'tidyverse' (Wickham et al., 2019), 'moments' (Komsta & Novomestky, 2022), 'glmmTMB' (Brooks et al., 2017), 'DHARMA' (Hartig, 2022), and

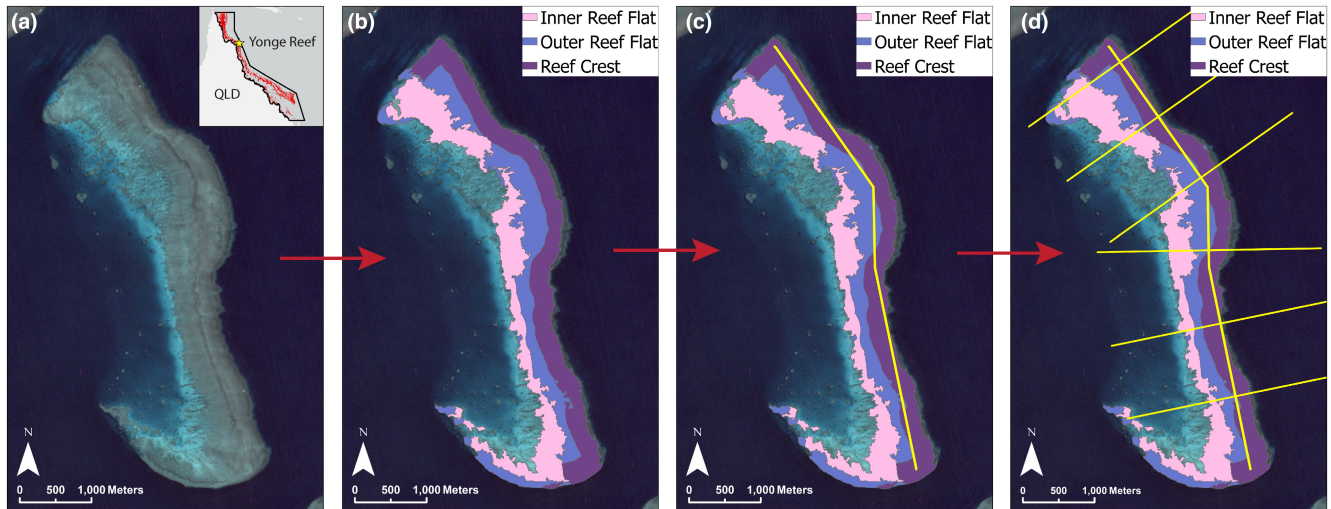
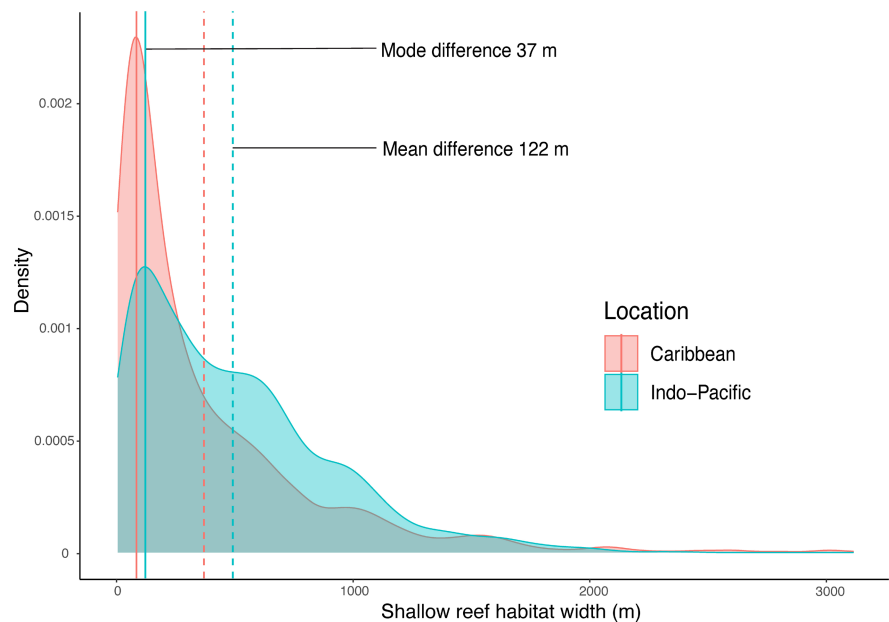


FIGURE 3 Process and methodology of shallow reef habitat width estimation. (a) Access high-resolution PlanetDove imagery and geomorphic maps through the Coral Allen Atlas (Yonge Reef, Northern GBR, AUS), (b) filter for desired reef zones, (c) create polyline (yellow) along the crest of the reef, and (d) create equally spaced cross-reef transects every kilometre along the polyline.

FIGURE 4 Kernel Density Estimates of shallow reef widths (m) in the Caribbean (red) ($n = 1945$ transects) and Indo-Pacific (blue) ($n = 1820$ transects). Dashed lines represent the means and solid lines the modes of the shallow reef widths in the Caribbean and Indo-Pacific (shallow reef habitat widths = inner reef flat + outer reef flat + reef crest).



'vegan' (Oksanen et al., 2022) packages. Relationships between the various reef zone widths and independent variables, including location (Caribbean vs. Indo-Pacific), exposure status (leeward vs. windward), and reef type (atoll, barrier, low or high island), were assessed using a principal component analysis (PCA). The PCA was performed on a correlation matrix. Kernel densities were estimated using the *density* function to visualize and compare mean, as well as modal, shallow reef habitat width patterns. We used a generalized linear mixed effect model (GLMM) to assess the nature of the relationship between the shallow reef habitat width and location. Location was used as a fixed effect, while reef and transect ID were fitted as nested random effects. The most parsimonious model was chosen based on the Akaike information criterion (AIC) and was fitted using a tweedie distribution with a log

link. Model assumptions were assessed using residual diagnostics and post-hoc pairwise means comparisons were conducted employing a Tukey's adjustment. While the relationship of shallow reef habitat width between locations was statistically insignificant (Supporting Information Table S2), we strongly caution against using this model as the extensive spatial autocorrelation in the dataset precluded detailed statistical comparisons (violating the assumptions of ANOVA and GLM or GLMM, as well as not meeting residual diagnostic standards) (Supporting Information Table S3). We, therefore, provide descriptive statistics and a multivariate analysis that can accommodate non-independent data. Further spatial autocorrelation and cluster analyses were conducted in the statistical analyses package GeoDa 1.4.1 (Anseling et al., 2006). See supporting information for details.

3 | RESULTS

The widths of shallow reef habitat (inner and outer reef flat and crest combined) in the Caribbean and Indo-Pacific ranged from 0m to over 3000m, although the vast majority are less than 500m wide (Figure 4). Interestingly, modal shallow reef widths between the two realms differed by only approximately 37m (estimated by kernel density estimates; 117.3m Indo-Pacific, 80m Caribbean). Averages likewise differ by just 122m ($486.9\text{m} \pm 9.4\text{m}$ Indo-Pacific, $365.1\text{m} \pm 9.9\text{m}$ Caribbean) (Figure 4). In both cases, Indo-Pacific

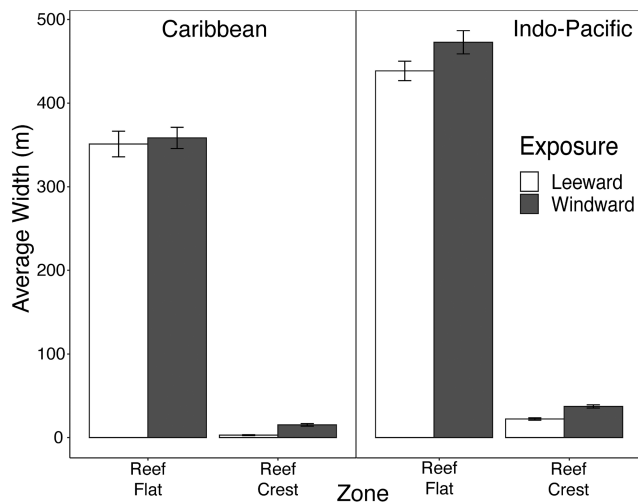


FIGURE 5 Average width (m) (\pm SE) of each geomorphic zone grouped by exposure to prevailing winds (white=leeward, grey=windward) across the Caribbean and Indo-Pacific realms Reef flats represent the combined data of inner flat and outer flat.

reefs were marginally wider than those in the Caribbean (Figure 4). Both realms exhibit right skewed distributions, with a greater prevalence of narrow width values; however, the Caribbean exhibits a stronger skew and relatively higher kurtosis than the Indo-Pacific (Figure 4) (see Supporting Information Table S4).

Generally, shallow reef systems in the Indo-Pacific were wider than their Caribbean counterparts. This holds true for total shallow reef width (Figure 4), and individual zone widths (reef flat and crest) (Figure 5). Reef flats (inner + outer reef flat) across both realms showed similar mean widths, ranging roughly between 350m and 475m regardless of their exposure status (Figure 5). Crests were by far the narrowest zone and again were wider in the Indo-Pacific and wider at windward sites in both realms (Figure 5). While windward sites seem to be marginally wider, total shallow reef habitat widths at windward versus leeward transects differed by just 29m on average (windward $436.9 \pm 9.8\text{m}$, leeward $408.1 \pm 9.8\text{m}$) (Supporting Information Table S5).

The patterns described above were strongly supported by the PCA, which explained over 90% of the total variance along its first two axes (Figure 6). The two realms showed substantial overlap, further emphasizing the overall trend of similarity in shallow reef habitat widths (Figure 6). However, the Indo-Pacific demonstrates larger variation along the PC2 axis, primarily driven by wider reef crests on the Great Barrier Reef (GBR), and generally wider shallow reef habitat zones (Figure 6). Notably, the loading vectors all orient in the same direction, signifying a shared increase in all habitats, that is, wider reefs have consistently wider individual zones (Figure 6). These patterns were also strongly supported by the geospatial analyses conducted in GeoDa which showed positive spatial autocorrelation (Moran's $I=0.694$ in the Caribbean and 0.674 in the Indo-Pacific)

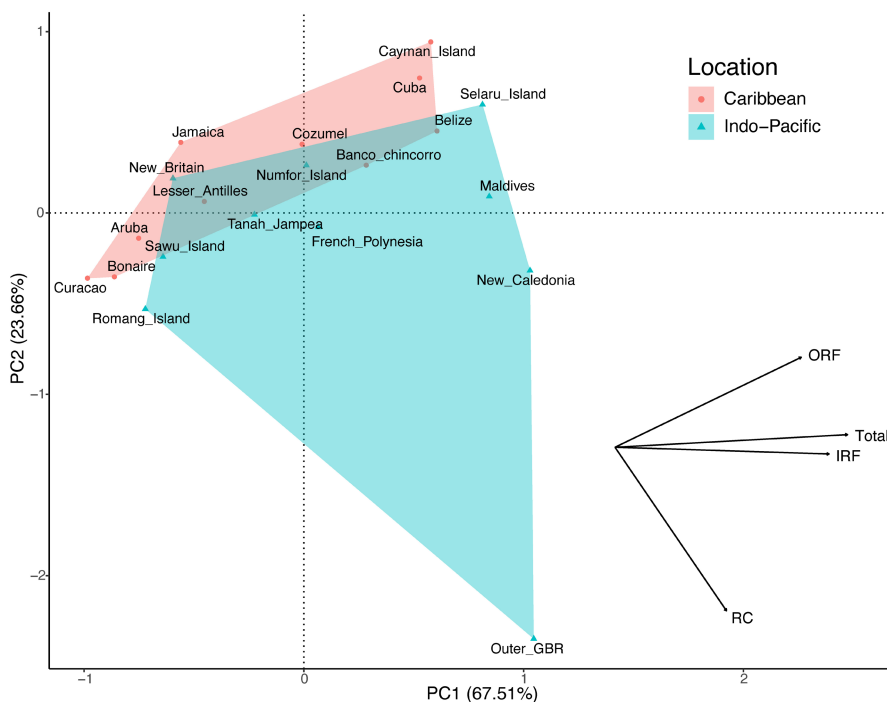


FIGURE 6 Principal component analysis (PCA) of the average widths of shallow reef habitat zones (vectors – IRF=Inner Reef Flat, ORF=Outer Reef Flat, RC=Reef Crest, Total=total shallow reef width) and their associated reefs based on their location. Circles and red hull: Caribbean, triangles and blue hull: Indo-Pacific.

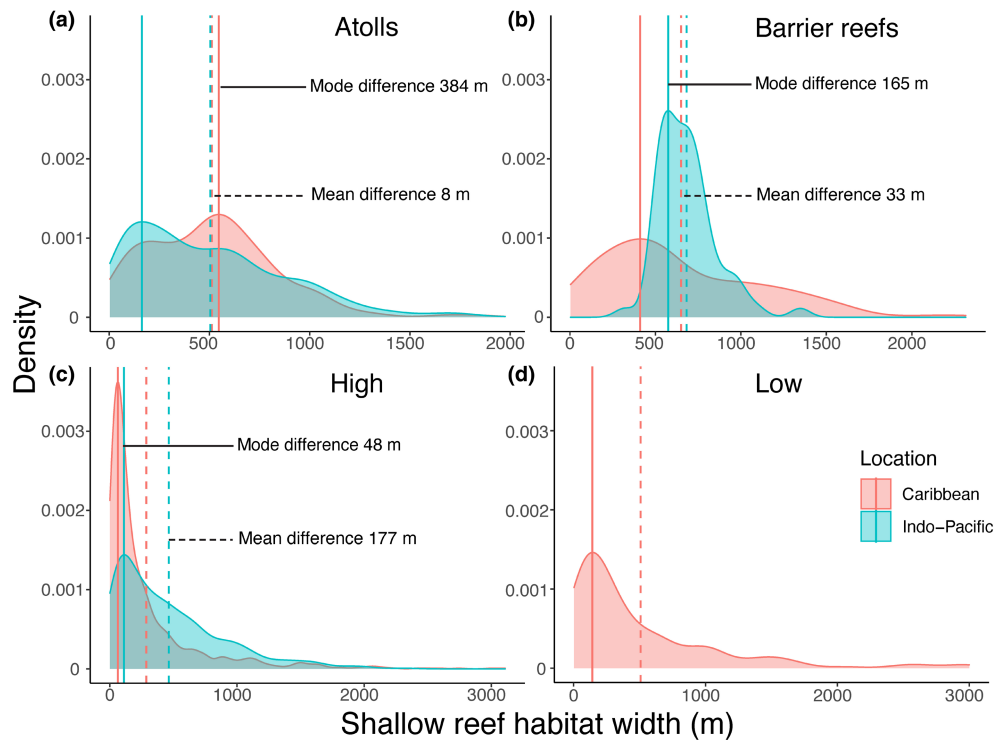


FIGURE 7 Kernel density estimates of shallow reefs widths (m) for (a) atolls, (b) barrier reefs, (c) high islands, and (d) low islands within the Caribbean (red) and Indo-Pacific (blue). Dashed lines represent the means and solid lines the modes of the shallow reef widths in the Caribbean (red) and Indo-Pacific (blue). Note the x-axes scales differ between the panels.

with narrow reef zones clustered together and wide zones clustered near other wide zones (Supporting Information Figures S1 and S2).

The average width also varied across the different reef types (Figure 7, Supporting Information Figures S3 and S4). Within reef types, shallow reef width averages and distributions show notable similarities, especially atolls (Figure 7a). Remarkably, mean shallow reef habitat widths of transects across atolls in the Indo-Pacific ($n=710$) and Caribbean ($n=261$) vary by just 8 m, averaging 503.7 m (± 14.3 m) and 511.7 m (± 19.9 m), respectively (Figure 7a). Furthermore, the Kernel Density estimates are very similar, showing slightly different modes but with substantial overlap in the distributions (Figure 7a). By contrast, the kernel density estimate distributions of shallow reef habitat widths of barrier reef systems in the Caribbean differ markedly from the Indo-Pacific (Figure 7b). Although average widths across barrier reef systems in the Indo-Pacific ($n=63$) and Caribbean ($n=151$) vary by less than 33 m (Figure 7b), the Indo-Pacific barrier reefs show a narrower range, averaging 682.6 m (± 21.5 m), while their counterparts in the Caribbean show a broader range and average 649.9 m (± 37.7 m) (Figure 7b). By contrast, reefs around high islands show a broader distribution in the Indo-Pacific ($n=1047$), averaging 463.7 m (± 13.1 m) (Figure 7c) when compared to their counterparts in the Caribbean ($n=1356$) which have a mean shallow reef habitat width of 286.7 m (± 10.9 m); their modal classes vary by just 48 m (Figure 7c). Lastly, low islands are absent from our Indo-Pacific dataset and average 507.4 m (± 45.4 m) in the Caribbean ($n=177$) (Figure 7d). Overall, while there is some

variation in the shape of kernel distributions, and in the biogeographical location of the reefs with the largest modes or means, the overall pattern is one of remarkably similar sizes, especially in atolls.

4 | DISCUSSION

This study represents a preliminary description of the biogeography of coral reefs as biogenic structures. Using novel remotely sensed data, we revealed that, in general, shallow reef habitats in the Indo-Pacific were only marginally wider than in the Caribbean, with the modal widths between the two realms diverging by just 37 m and means by a mere 122 m. This pattern is consistent with our expectations, in direction, but not in extent. As described in the introduction, we hypothesized that total shallow reef habitat widths in the Indo-Pacific should be considerably wider than in the Caribbean (at least 500 m wider). The unexpected similarity in widths between the two realms suggests that species richness, sea-level regime and biogeographical history have a limited impact on reef growth, and that other factors may be more important in constraining the size of biogenic coral reef structures. These factors may include (1) antecedent topography of the Pleistocene substratum, (2) non-coral components as drivers of reef growth or (3) local hydrodynamics. Below, we discuss these factors and their implications for our understanding of reef accretion (i.e. lateral and/or vertical reef growth) and the future of coral reefs.

4.1 | Antecedent topography

Today, it is widely understood that during the Holocene many reefs initiated their accretion and reef formation on Pleistocene reef substrata (Hopley et al., 2007; Montaggioni & Braithwaite, 2009). Thus, it has been hypothesized that the extent and nature of these Pleistocene foundations may govern the physiography of Holocene and modern coral reef structures (Barrett & Webster, 2012; Gischler & Hudson, 2004; Grigg et al., 2002; Purdy, 1974). More specifically, the literature suggests that the unique morphology, size, and shape of both atolls and barrier reef systems are predominantly produced by the subaerial exposure of relic Pleistocene substrata (Davies, 2011; Droxler & Jorry, 2021; Montaggioni & Braithwaite, 2009). For instance, Pirazzoli and Montaggioni (1986) found that the reticulated lagoon at Mataiva Atoll in the central Pacific, which is divided into a series of central basins, is a result of extensive sub-aerial exposure of the antecedent Pleistocene platform. Consequently, the similarity in average shallow reef widths in both atoll and barrier reef systems across both realms in this study could potentially be a result of similar sub-aerial exposure regimes during the Pleistocene. However, on more local scales, Holocene reef growth can occur independently, without the restrictions of antecedent topography (Montaggioni & Braithwaite, 2009; Salas-Saavedra et al., 2018). In his study on John Brewer Reef in the central GBR, Walbran (1994) found that modern morphologies of coral reef structures may result from the interactions between Holocene sea-level rise, prevailing hydrodynamics, and the biological activity of organisms in response to these other factors. Thus, modern coral reef structures appear to be the result of a complex suite of interactions between the biology and diversity of reef-dwelling organisms within the context of prevailing hydrodynamic or environmental drivers. This may be influenced, but is not necessarily constrained, by the underlying Pleistocene substratum (Adey, 1978; Walbran, 1994).

4.2 | Coral growth driving reef accretion (vertical and lateral)

Coral reefs throughout the world share the ability to create three-dimensional, biogenic structures through the accumulation of calcium carbonate. Given the markedly different coral lineages, and the 14-fold difference in coral species richness between the two realms, reefs in the Indo-Pacific were expected to exhibit much more extensive reef growth, both vertically and, once sea level has been reached, laterally. However, our results reveal that the difference in shallow reef habitat widths between Caribbean and Indo-Pacific reefs was not as pronounced as anticipated. Reef accretion, as indicated by present-day reef widths, did not appear to be influenced strongly by coral biodiversity. Furthermore, throughout the Holocene, both realms showed similar historical rates of vertical carbonate accretion. While Caribbean reefs accreted between 3 mm and 4 mm/year (Hubbard, 2009), reef accretion rates in the Indo-Pacific were only slightly below that average (~3 mm/year; Dullo, 2005). However,

Holocene reef development models assume that reef accretion is directly controlled by the growth rates of the local dominant coral species, implying that reefs dominated by branching species would accrete faster than reef systems dominated by slow-growing massive coral species (Adey, 1978; Chappell, 1980; Gischler, 2008). Recently, Roff (2020) used cores from two opposing reef slopes at an inshore reef on the central GBR to explore reef accretion patterns of late-Holocene reef frameworks. While the two sites were dominated by different coral species, *Goniopora* and *Acropora*, that show a 10-fold difference in potential growth capacity, core data revealed that vertical reef accretion rates were strikingly similar over the last 750 years (Roff, 2020). Similarly, in the Caribbean, there was no significant difference in reef accretion rates between reefs dominated by fast-growing and slow-growing coral species (Gischler, 2008; Hubbard, 2009). Moreover, using fossil data, Johnson et al. (2008) showed that Caribbean reef development remained unaffected by an extinction event in the late Pliocene that decreased coral diversity by 50%. Thus, one of the key coral reef functions, reef accretion (a function being defined as the movement or storage of energy or material; sensu Bellwood et al., 2019), appears to be largely unaffected by variation in biodiversity. Reef growth (accretion) appears to be primarily driven by abiotic and biotic interactions with the environment (Johnson et al., 2008).

At Holocene time scales, coral growth and reef accretion may be decoupled processes; challenging the common assumption that the life history and growth capabilities of corals dictate reef accretion rates (cf. Hammerman et al., 2022; Roff, 2020). Consequently, it has been suggested that past research may have overestimated the role of in situ coral growth in reef building processes (Blanchon et al., 2017; Hammerman et al., 2022; Hubbard et al., 1990; Perry et al., 2012). The similarities in shallow reef widths in the Caribbean and Indo-Pacific, despite highly disparate coral assemblages, support this emerging perspective. Our findings suggest that net reef accretion (both vertically and/or laterally) and coral diversity are not strongly linked. This may indicate a potential separation between biodiversity and a key reef function (i.e. reef growth). Indeed, the accumulation of stressors on coral reefs in the Anthropocene may cause further decoupling of the processes that support reef accretion from the more visible ecological coral-based processes that appear to drive carbonate production on the reef surface (Morais et al., 2022).

Coral reef accretion may be facilitated through a multitude of other, non-coral growth processes and by other non-coral organisms. Recently, Hammerman et al. (2022) showed that a large percentage of investigated reef slopes in the Red Sea were not constructed solely by in-situ coral growth, with a considerable contribution from unconsolidated coral rubble. Similarly, in St. Croix, US Virgin Islands, Hubbard et al. (1990) described the local reef framework as a 'garbage pile' of carbonate reef detritus rather than an array of in situ coral framework assemblages. Montaggioni (2005) likewise identified coral and skeletal rubble facies as the most prominent features of reef cores in the Indo-Pacific, occupying up to 60% of the total core volume, while Morais et al. (2022) showed that dead

coral skeletons may have a negligible contribution to local, in situ, reef accretion.

If corals do not contribute to reef accretion as much as previously assumed, other organisms may underpin reef accretion. Crustose coralline algae (CCA), for example, have been shown to be key secondary reef builders, able to consolidate and cement reef framework (Littler & Littler, 2013), thus playing an important role in reef accretion (Nash et al., 2013). Kench et al. (2022) showed that vertical reef accretion in the low coral cover wave breaking zone (reef crest) was maintained, even shortly after periods of elevated sea-surface temperatures, by CCA calcification. Within 2 years of a major bleaching event, the outer rim of the reef flat and reef crest maintained positive accretion rates that, averaging up to 6.6 mm/year vertical growth, matching pre-bleaching values (Kench et al., 2022). Reef accretion may therefore still occur in disturbed areas lacking live coral cover. Vertical accretion rates appear to be predominantly influenced by local environmental factors, rather than by the local abundance or diversity of corals. Clearly, the future of coral reefs will also depend on the response of these non-coral taxa to climate change. However, our understanding and knowledge regarding the potential responses of these non-coral organisms to climate change, and ultimately, their capacity to facilitate reef growth in the future, remains limited (Short et al., 2015). Addressing the knowledge gaps surrounding the non-coral components of reef vertical and lateral accretion will be vital to predicting the impacts of climate change on biogenic coral reef structures.

4.3 | Local hydrodynamics as a common factor

While limited in number, studies investigating mid-late Holocene coral assemblages and their living counterparts across reefs in the Indo-Pacific and Red Sea have found little variation in overall composition and diversity (Hallmann et al., 2020; Pandolfi & Minchin, 1996; Roche et al., 2011). This suggests that over the course of the Holocene, environmental parameters—such as light conditions or nutrient levels, have changed relatively little, except within the context of sea-level-driven hydrodynamic regimes (Hallmann et al., 2020).

The importance of hydrodynamics has been established for other reefal structures, such as reticulate ridges in reef systems (Schlager & Purkis, 2015) and sand aprons (Isaack & Gischler, 2017). However, the degree to which modern reef morphology can be attributed to prevalent hydrodynamics remains relatively poorly understood (Camoin & Webster, 2015; Salas-Saavedra et al., 2018; Woodroffe & Webster, 2014). While reef structures on the GBR show vast differences in their timing of initiation and rate of accretion during the early phases of reef development, once sea level was reached, they appear to be strikingly similar (Dechnik et al., 2015, 2017; Salas-Saavedra et al., 2018). This concept is underlined by the results in this study where isolated carbonate platforms, such as atolls and barrier reef systems, showed remarkably similar average widths between biogeographical realms. This emphasizes the potential role

of local hydrodynamics in shaping, and potentially homogenizing, modern reef structures and their morphology. It also suggests that the influence of hydrodynamics on reef accretion at sea level may be a common factor shaping and constraining reef growth (Dechnik et al., 2016, 2017; Salas-Saavedra et al., 2018), independent of biogeographical location or geological time period.

Recently, Rankey (2021) investigated the interactions between geomorphology and hydrodynamic setting to assess reef progradation patterns on isolated carbonate platforms and atolls. He noted that sand aprons on the windward side are generally wider due to the higher energy across these locations. This is consistent with the existing literature (Hongo & Kayanne, 2009; Yamano et al., 2003) and the findings herein, which showed consistently wider shallow reef habitats along exposed, windward, margins. However, sand apron development, and more generally reef progradation, has been shown to be self-limiting (Ortiz & Ashton, 2019; Rankey, 2021; Vila-Concejo et al., 2022). As reef flat and sand apron widths increase, shear stress decreases to a point where no sediment can be moved by hydrodynamic forces (Rankey, 2021). Early work also suggested that the reefs' ability to prograde lagoonward would be limited by extreme temperatures, turbidity, and salinity in lagoons, which may exceed coral reef growth thresholds (Neumann & Macintyre, 1985). Therefore, the shallow reef habitats of atolls and other isolated carbonate platforms may reach a width that ultimately halts leeward accretion. Seaward accretion is also likely to be limited by the steepness of the reef slope (Duce et al., 2020; Kan et al., 1995; Maxwell, 1968). These factors potentially explain the homogeneous distribution of shallow reef habitat widths documented herein for atoll systems in the Caribbean and Indo-Pacific. Indeed, prevailing hydrodynamics may be the primary driving force underpinning the similarity of widths in all the coral reef structures examined in the Caribbean and Indo-Pacific. Hydrodynamics may be a universal factor that overrides the biogeographical, historical, and evolutionary contingencies between these two distinct realms.

5 | CONCLUSION

This study demonstrates that the widths of shallow-water biogenic coral reef habitats in the Caribbean and Indo-Pacific are strikingly similar. Although these two realms have highly disparate biogeographical extents, biodiversity patterns, evolutionary and sea-level histories, their modal shallow reef zone widths differed by just 37 m. This suggests that there are other, non-historical, drivers underpinning this striking similarity; drivers that can override the influence of biogeography and sea-level history. Furthermore, the results of this study may lend support to the suggestion that reef accretion, a geological process, is largely decoupled from coral growth, an ecological process, with the corollary that coral diversity does not determine reef accretion rates. Once biogenic coral reef structures reach sea level, hydrodynamic forcing appears to be the major force in a self-limiting system that constrains reef accretion. While climate change is driving the global loss of corals, the results of this study emphasize

the need for a more thorough understanding of the contributions of non-coral components to coral reef accretion and other ecosystem functions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code used for analysis are freely and publicly accessible at <https://doi.org/10.25903/29h0-w215>.

ORCID

Lucas L. Lutzenkirchen  <https://orcid.org/0000-0002-3606-5944>

David R. Bellwood  <https://orcid.org/0000-0001-8911-1804>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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