

Diversity and distribution of intertidal marine species in Singapore

Lionel Jian Wei Lim^{1#}, Joseph Boon Yeow Loh^{1#}, Aloysius Jin Shen Lim¹, Beryl Ying Xin Tan¹, Yin Cheong Aden Ip², Mei Lin Neo^{2,3}, Ria Tan⁴ & Danwei Huang^{2,3*}

Abstract. Singapore, located within the biodiverse tropical Southeast Asia, hosts a high diversity of living species, including those thriving in marine habitats such as corals reefs, seagrass meadows, as well as rocky and sandy shores. While its dramatic transformation in the last 200 years has resulted in the loss of natural habitats and their associated marine species, coastal flora and fauna appear to be persisting. Research on the spatial variation of local marine biodiversity remains limited in geographic and taxonomic coverage. In this study, we consolidated existing data on species richness of 27 intertidal sites in Singapore obtained by researchers and citizen scientists since the year 2000, and performed diversity and community analyses to characterise spatial patterns in species richness and composition around its shores. Our dataset contains a total of 994 intertidal marine species comprising macroflora, macrofauna, and macroalgae, and analyses show that sites along the Johor Straits in the north and Singapore Strait in the south are not significantly different in richness. When aggregated across sites, however, there are more species in the south than in the north likely due to the wider range of habitat types along the Singapore Strait. Community composition is also significantly different between northern and southern sites as a result of these distinct habitats. Interestingly, hardening of the shoreline, especially along the southeastern coast, have created novel habitats for coral and coral-associated communities to develop. Better understanding of these diversity drivers will help scientists and resource managers prioritise intertidal areas and devise strategies for coastal conservation.

Key words. biodiversity, citizen science, community composition, Johor Straits, Singapore Strait, tropical coastal habitats

INTRODUCTION

Singapore is situated in tropical Southeast Asia, a region known to be the epicentre of marine species richness (Allen & Werner, 2002; Hoeksema, 2007; Bellwood et al., 2012). Apart from the large number of living species, the region also hosts a high diversity of ecosystems (Chou, 1994; Morton & Blackmore, 2001; Burke et al., 2002). Correspondingly, the marine environment of Singapore consists of many different types of habitats, including coral reefs found mainly at the southern islands, seagrass meadows dispersed widely but ephemerally on sandy shores, and mangrove forests scattered largely along the northern coast with smaller patches in the southern islands (Fig. 1) (Tan et al., 2016a). Altogether, 3,650

shallow marine invertebrates, fishes, and plants have been recorded in Singapore's coastal waters (Wells et al., 2019), including species described from here nearly two centuries ago (Dana, 1846; Milne Edwards & Haime, 1849, 1851).

During the intervening years, Singapore's natural landscape had undergone a dramatic transformation mainly due to its burgeoning population and development into a global shipping hub (Chou et al., 2019). In particular, much of the coastal areas—along the mainland and its surrounding islands—have been heavily modified, resulting in the destruction of many marine habitats and intensification of chronic urbanisation stressors (Hilton & Manning, 1995; Chou, 2006; Tay et al., 2018). For example, from 1922 to 1993, areas of coral reefs and mangroves were reduced by nearly 50% and over 90%, respectively (Lai et al., 2015). Consequently, local losses of marine species are apparent (e.g., Huang et al., 2009; Neo & Todd, 2012a; Yip et al., 2018; Poquita-Du et al., 2019).

Despite these impacts, coastal flora and fauna appear to be persisting, accompanied by a greater understanding of local marine biodiversity driven by the increased sampling and observational efforts over the last two decades (Tan et al., 2016a; Wells et al., 2019). While much of the research has been focused on more well-known organisms such as corals (Huang et al., 2009; Wong et al., 2018; Chow et al., 2019; Ng et al., 2019) and fishes (Low & Chou, 1994; Low et al., 2009; Low, 2013), intensive sampling campaigns such as the

Accepted by: Toh Tai Chong

¹Anglo-Chinese Junior College, 25 Dover Close East, Singapore 139745, Singapore;

[#]These authors contributed equally to this work

²Department of Biological Sciences, National University of Singapore, 16 Science Drive 4, Singapore 117558, Singapore; Email: huangdanwei@nus.edu.sg (*corresponding author)

³Tropical Marine Science Institute, National University of Singapore, 18 Kent Ridge Road, Singapore 119227, Singapore

⁴WildSingapore, c/o Lee Kong Chian Natural History Museum, Faculty of Science, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Singapore

Comprehensive Marine Biodiversity Survey (CMBS) during 2010–2015 (Tan et al., 2015, 2016b) as well as sustained surveys by citizen scientists (Fautin et al., 2009; Oh et al., 2019) have contributed numerous valuable biodiversity observations. Although many surveys have been conducted to document the richness of marine flora and fauna around Singapore, there has been hardly any analysis focusing on the spatial variation of species richness with a broad geographic and taxonomic coverage. Such research aiming at generating insights into the spatial correlates of biodiversity will help scientists and resource managers prioritise intertidal areas and devise strategies for coastal conservation and management.

Currently, large numbers of species records are available to conduct more spatially and taxonomically expansive studies, especially for intertidal environments which consist of the most accessible marine sites. These data may be derived from published data, grey literature, as well as unpublished observations. In particular, there exist nearly two decades' worth of observational data for hundreds of marine species contributed by numerous researchers and citizen scientists, which are available as the Wild Fact Sheets (WildSingapore; <http://www.wildsingapore.com/wildfacts>; Fautin et al., 2009; Oh et al., 2019). This rich resource has neither been analysed nor integrated with published scientific data to more precisely estimate the marine biodiversity of Singapore. More generally, existing intertidal biodiversity studies in Singapore are limited to the characterisation of a few major groups of marine species at spatially-restricted scales (e.g., Huang et al., 2006a, b; Lee et al., 2009a, b; 2012; Tan & Yeo, 2010; Yaakub et al., 2013).

We here aim to compile, verify, and analyse the species records in the Wild Fact Sheets resource to better understand the spatial distribution of intertidal marine species in Singapore. Specifically, we seek to identify the differences in species diversity among sites, such as between northern (Johor Straits) and southern (Singapore Strait) coasts. Due to a greater range of habitat types in the latter, particularly with the structurally complex coral reefs adjacent to the southern islands (Tan et al., 2016a; Wong et al., 2018; Chou et al., 2019), it is expected that the southern sites will be more species-rich and compositionally distinct compared to sites along the northern shores. Our comparisons show that community composition, but not species richness, is statistically different between the northern and southern sites, with the variations broadly attributable to dissimilarities in habitat types and environmental patterns.

MATERIAL AND METHODS

We consolidated diversity and distributional data which were contributed by numerous researchers and citizen scientists, who made observations of marine species at 27 intertidal sites—10 northern (Johor Straits) and 17 southern (Singapore Strait) (Fig. 1)—between 2000 and 2018 (e.g., Oh et al., 2019). The data were obtained through approximately 40 field trips made annually, with each intertidal site visited at least once per year mostly by citizen scientists and

occasionally joined by professional researchers. During each site visit, a minimum of two observers walk the entire expanse of the intertidal area for 1.5–3.0 hours, depending on the tidal range of the day. Macroflora, macrofauna, and macroalgae were recorded mainly by taking photographic images of organisms, although later surveys generally focused on the rarer and more interesting taxa. Observational data were supported by the images uploaded onto the Wild Fact Sheets database (<http://www.wildsingapore.com/wildfacts>). The curation of images and sighting information after field trips was performed only by R. Tan to ensure consistency. For this study, the names of intertidal sites followed that of the database.

Data were transcribed into separate spreadsheets according to major taxa to record the presence and absence of each species at the respective sites. Since many species were not listed with formal taxonomic names, images linked to each species record were reviewed based on morphology and verified or reassigned to the correct identity where necessary, thus ensuring that species recognition was consistent across all observational records. Following species identity verification, spreadsheets were combined into a community data matrix for diversity analyses. Data are available at Zenodo (<http://dx.doi.org/10.5281/zenodo.3463489>).

Species richness for each site was computed and compared between the northern and southern sites using the Welch t-test, following the Shapiro-Wilk test and F-test for normality and homogeneity of variances, respectively, in R version 3.6 (R Core Team, 2013). Variation of community composition between the northern and southern sites was examined using non-metric multidimensional scaling (NMDS) with the Jaccard distance measure (Jaccard, 1901), and tested using analysis of similarities (ANOSIM) in the vegan package version 2.5 (Oksanen et al., 2013).

RESULTS AND DISCUSSION

Our dataset consolidates a total of 994 intertidal marine species (i.e., macroflora, macrofauna, and macroalgae) from 27 intertidal sites (Fig. 1). The most widespread species are fishes, specifically the orange-spotted rabbitfish (*Siganus guttatus*) and stripe-nosed halfbeak (*Zenarchopterus buffonis*) which are present at all sites across both northern and southern shores. The sites with the richest intertidal assemblages are Pulau Semakau (SM) and Chek Jawa (CJ) with 520 and 487 species recorded respectively. By contrast, the sites with the fewest species are Sungei Buloh (SB) and Lim Chu Kang (LC), which host 69 and 20 species respectively (Fig. 2). Although the four most species-poor sites are from the north—including Sungei Buloh and Lim Chu Kang—and the mean richness of northern sites (mean = 244 ± SD 161) is lower than that of southern sites (mean = 352 ± SD 88), their difference in richness is not significant ($t = -1.96$, d.f. = 12.2, $p = 0.0732$).

The range of richness values among northern sites (minimum = 20, maximum = 487) is much larger than among the

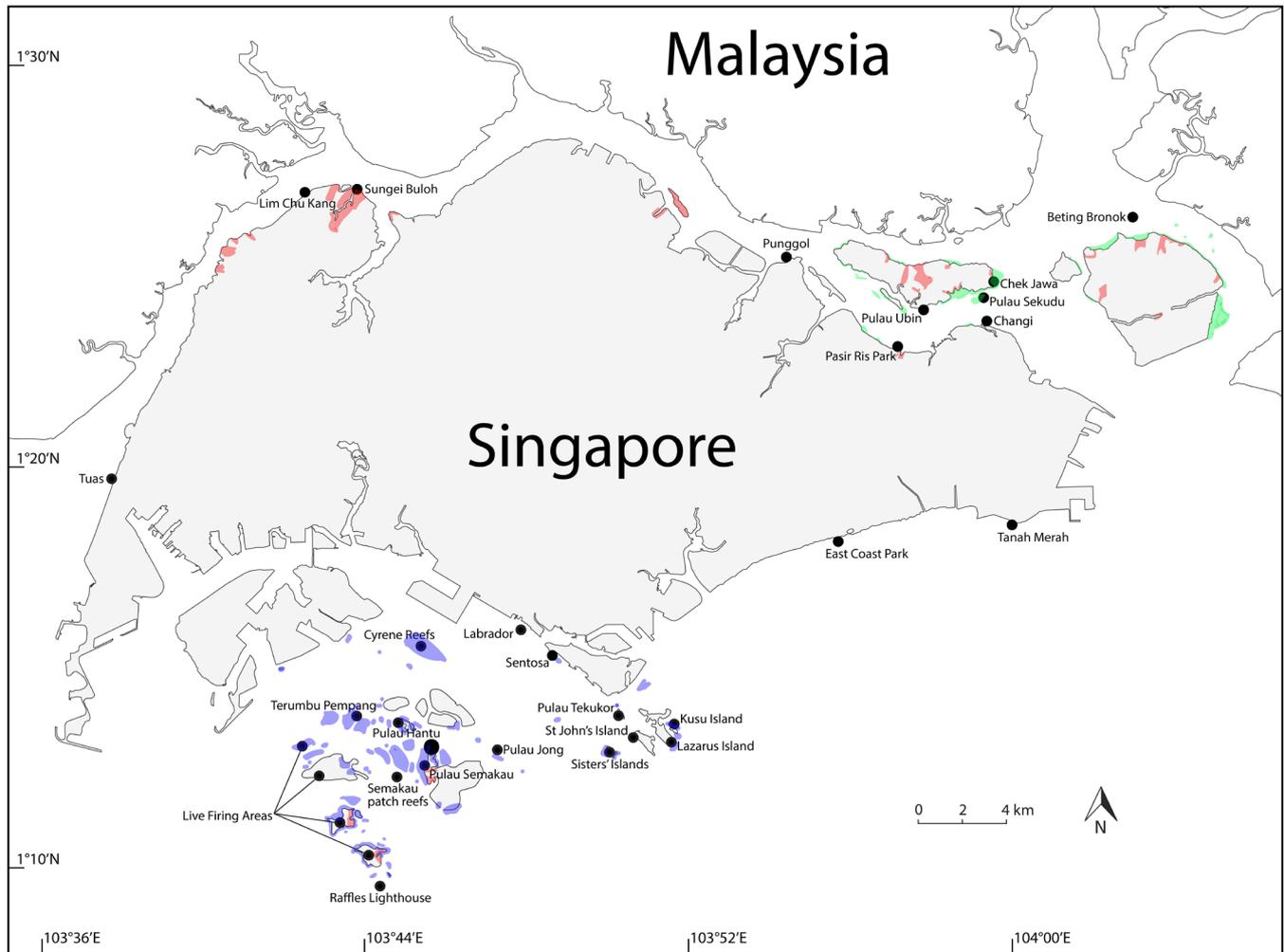


Fig. 1. Map showing coastal sites analysed in this study. Distribution of coral reefs, mangrove forests, and sand/mudflats shaded in purple, red, and green, respectively, according to Lai et al. (2015).

southern sites (minimum = 193, maximum = 520) and are largely overlapping, thus explaining the negligible difference detected. The large disparity in species richness in the north is partly attributable to the relatively few marine species recorded in the mangrove sites, Sungei Buloh and Lim Chu Kang. Mangroves here are diverse ecosystems (Low et al., 1994; Ng & Low, 1994), but they are dominated primarily by estuarine and terrestrial species (Ng & Sivasothi, 1999a, b; Tan, 2013). Since our dataset focused only on coastal marine species, the analysis underestimates the biodiversity residing in estuarine sites such as Sungei Buloh and Lim Chu Kang, even as it gives a representative picture of marine flora and fauna. Addition of a comprehensive catalogue of estuarine species to our dataset, particularly the angiosperms (Ng & Sivasothi, 1999a; Sheue et al., 2005) and insects (Murphy, 1990; Tan, 2013), would benefit future studies aiming to characterise overall mangrove diversity.

While we find no statistically significant difference in the number of species at the site level between the northern and southern coastal areas, there are more species aggregated among all southern sites ($n = 891$) compared to the northern sites ($n = 731$). It is also apparent that species richness is higher in the south for nearly all major taxa (Fig. 3). The Johor Straits are generally shallow with depths averaging

between 8 and 10 m (Sin et al., 2016), with the flow and mixing of water limited among the northern sites due to the Johor-Singapore Causeway that was built across the Straits about a century ago (Bird et al., 2004; Friess et al., 2012). Restricted tidal currents as well as nourishment from sediment delivered into the Straits by large river systems in Johor and Singapore (Friess et al., 2012; Phang et al., 2015; Sin et al., 2016) have resulted in the estuarine northern shores being fringed primarily by mangroves, mudflats, and sandflats (Tan et al., 2016a). By contrast, the wider Singapore Strait has an average depth of 30 m and an irregular seabed with many islands and shoals (Sin et al., 2016), thus encompassing a wider range of marine habitats (Tan et al., 2016a). The more diverse abiotic environment in the Singapore Strait likely accounts for the higher species richness among the southern sites.

The disparity in diversity is especially pronounced for Scleractinia and Corallimorpharia (Fig. 3), which are known to preferentially inhabit coral reef environments found along the southern shores (Chuang, 1961, 1977; Huang et al., 2009; Oh et al., 2019). Specifically, shallow reef habitats are found surrounding the islands and on tidally-exposed patches along the Singapore Strait, but coral communities are also found along seawalls and the last remaining rocky

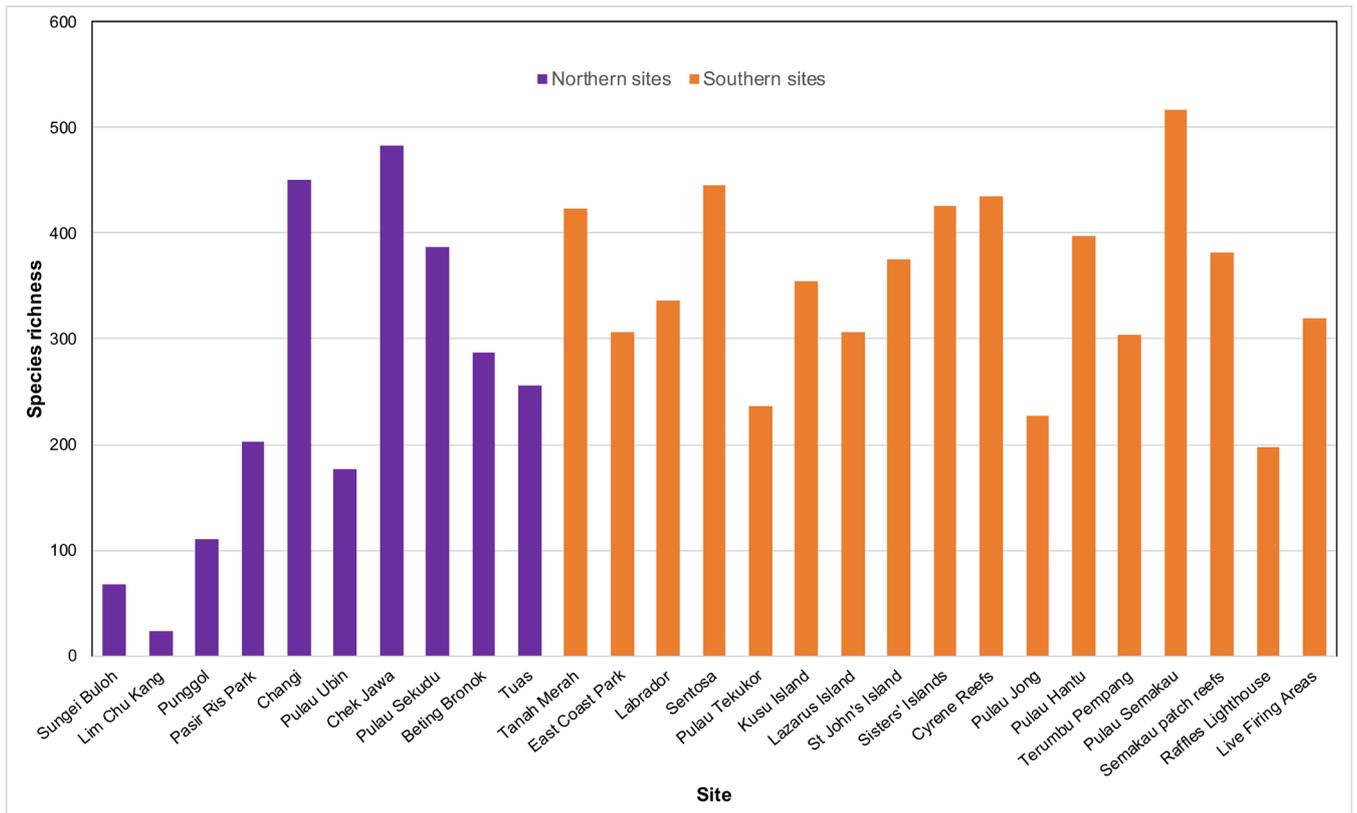


Fig. 2. Species richness of intertidal sites in Singapore.

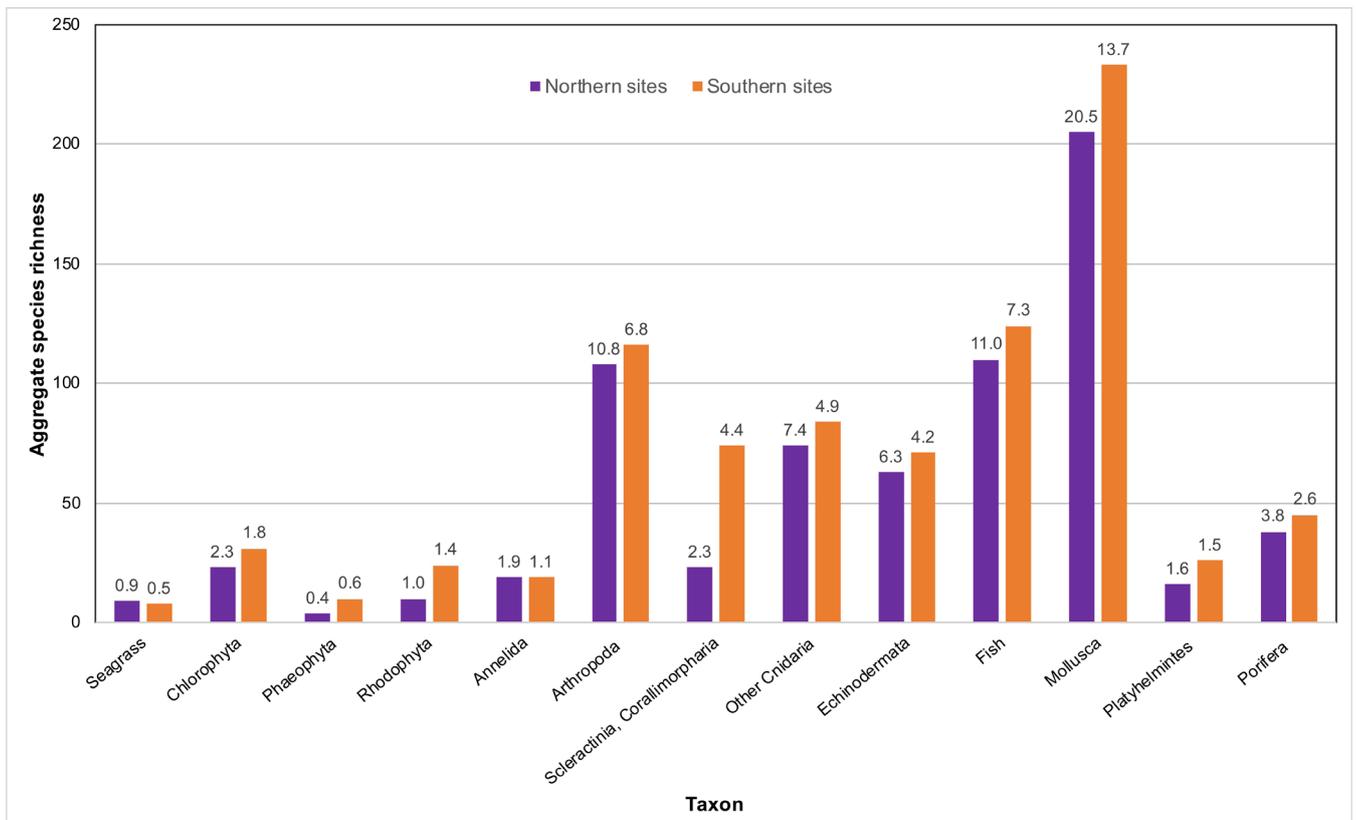


Fig. 3. Species richness of major taxa aggregated across northern and southern intertidal sites separately. Values above bars indicate aggregate species richness normalised by the number of sites.

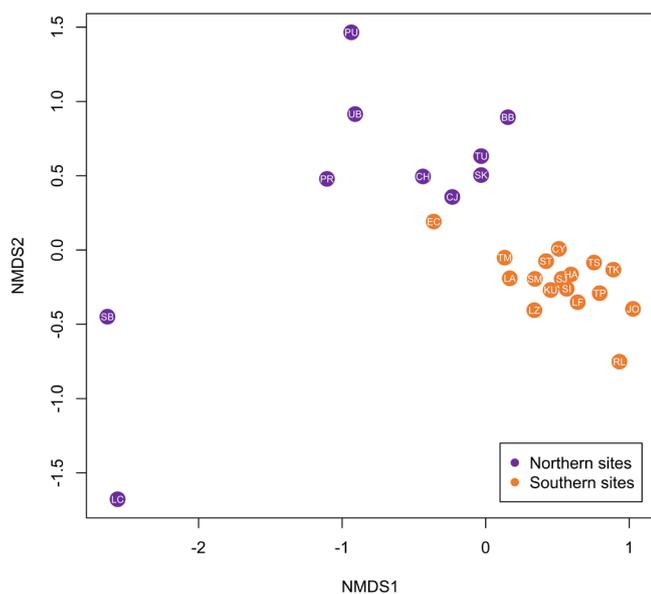


Fig. 4. Non-metric multidimensional scaling (NMDS) of intertidal marine communities in Singapore, based on the Jaccard distance (stress = 0.0652). SB: Sungei Buloh; LC: Lim Chu Kang; PU: Punggol; PR: Pasir Ris Park; CH: Changi; UB: Pulau Ubin; CJ: Chek Jawa; SK: Pulau Sekudu; BB: Beting Bronok; TU: Tuas; TM: Tanah Merah; EC: East Coast Park; LA: Labrador; ST: Sentosa; TK: Pulau Tekukor; KU: Kusu Island; LZ: Lazarus Island; SJ: St John's Island; SI: Sisters' Islands; CY: Cyrene Reefs; JO: Pulau Jong; HA: Pulau Hantu; TP: Terumbu Pempang patch reefs; SM: Pulau Semakau; TS: Semakau patch reefs; RL: Raffles Lighthouse; LF: Live Firing Areas.

shore (Labrador Beach) on the mainland (Todd & Chou, 2005; Huang et al., 2006a; Wong et al., 2018). For most other taxon groups, the greater number of sites surveyed may have contributed to the higher richness recorded in the south, since the differences are nominal when considering the number of sites (Fig. 3). Relatedly, aggregate species richness for seagrasses and annelids is equal or higher in the northern sites due to the predominantly sandy and muddy environments along the Johor Straits, which are preferred by these organisms (Tan & Chou, 1993; Yaakub et al., 2013, 2014; Glasby et al., 2016). Taken together, our results show that habitat type and distribution influence species richness of various taxa to a large extent.

Apart from species diversity, intertidal community composition differs significantly between northern and southern sites (ANOSIM, $R = 0.7285$, $p = 0.001$). The NMDS show a clear distinction between them (Fig. 4) despite the non-significant difference in site-wise species richness. It is also clear from the distribution of data points on the NMDS that the northern communities are generally more distinct from one another as compared to those in the southern sites. Much of this variation is contributed by the two mangrove sites, Sungei Buloh and Lim Chu Kang, which host mainly estuarine and terrestrial species (Ng & Sivasothi, 1999a, b; Tan, 2013). Aside from these sites, there is no evidence of clustering according to geographic proximity in the north, especially since the intertidal community at Tuas (TU) is nestled amongst sites in the eastern Johor Strait even though it is physically situated in the western Johor Strait.

Similarly, intertidal communities at the southern sites are not clustered by geographic proximity except for Raffles Lighthouse (RL). This pattern is not surprising considering the relatively large spatial separation between Raffles Lighthouse and the other southern sites (Fig. 1). Furthermore, Raffles Lighthouse and Pulau Jong (JO) are the smallest islands surveyed in the south, thus accounting for the relatively low species richness (Fig. 2) and distinction in community composition (Fig. 4). East Coast Park (EC) and Tanah Merah (TM), although not clustered away from the rest of the southern sites, have the most similar assemblages to the northern sites. These sites can be considered novel habitats as they constitute reclaimed land. Much of the sandy shores along East Coast Park today, for instance, had established following the 'Great Reclamation' in the 1960s that added 1,525 ha of land in the area (Housing Development Board, 1963; The Straits Times, 1983; Poquita-Du et al., 2019). Prior to coastal development, these sites may have been much more similar to the northern sites in terms of habitat type since the sandy intertidal environment along Singapore's southeastern shore was contiguous with Changi (CH) in the north (Fig. 1) (Malaya Survey Department, 1954; Yaakub et al., 2014). Following the eastward land extension and construction of seawalls along these sites, many corals and coral-associated species have recruited and are thriving there (Wong et al., 2018), even as they retain flora and fauna which are characteristic of the Johor Straits wherever sandy patches remain. As a result, communities at East Coast Park and Tanah Merah are intermediate between the northern and southern localities (Fig. 4).

The Wild Fact Sheets database, driven mainly by contributions from citizen scientists, is the most up-to-date, publicly-available resource on intertidal taxa found in Singapore. The data have helped advance local biodiversity knowledge by facilitating taxonomic research on select groups such as Actiniaria (Yap et al., 2014, 2019), Corallimorpharia (Oh et al., 2019), Mollusca (Chim et al., 2009; Neo, 2010), and Echinodermata (Ong & Wong, 2015; Chan et al., 2018; Ong et al., 2019), as well as supporting field studies on species ecology (Lee et al., 2012; Neo & Todd, 2012a) and phylogenetics (Quek & Huang, 2019; Quek et al., 2019, 2020). When citizen science meets research, insights on the past, present, and future of species persistence and loss are deepened (e.g., Neo & Todd, 2012b; Poquita-Du et al., 2019). More practically, data and information available through resources such as the Wild Fact Sheets are valuable to scientific projects facing temporal and funding constraints (e.g., Kobori et al., 2016; Lau et al., 2019). Citizen science is clearly a promising approach to further our understanding of local marine biodiversity.

While the dataset analysed here represents a comprehensive range of marine species and coverage of localities along Singapore shores, continuing surveys are needed to increase the accuracy of species identification and richness estimates. Each record here is supported by geotagged photographs which can be verified in greater detail by professional taxonomists, although field images may still be deficient in terms of the diagnostic characters used to distinguish

species as compared to voucher specimens. There may also be potential taxonomic biases as volunteer surveyors may not note all the species encountered, either because they lack the expertise to recognise them (Dickinson et al., 2010), or they may have focused only on the rare and interesting taxa and neglected the more common ones (Tulloch & Szabo, 2012; van Strien et al., 2013). Future feedback by taxonomic experts, who may also apply modern techniques such as DNA barcoding (Chang et al., 2018; Wainwright et al., 2018), standardised sampling (Leray & Knowlton, 2015; Chang et al., 2020), and pattern analysis (Chan et al., 2019), would help enhance the identification accuracy of specific taxa. Experts may also be more targeted and precise in their observational approaches so that more organisms would be recorded. Quantification of species abundance—whether relative or absolute—and analysis of temporal variation would provide useful information on community diversity and biotic change over time (Obura et al., 2019).

Overall, our study has quantified broad spatial patterns of intertidal marine species in Singapore, based on a rich set of observations by researchers and citizen scientists. In particular, we show that aggregate richness and community composition are distinct between Johor Straits and Singapore Strait, although there is no statistically significant difference in the number of species at the site level. Patterns in community composition can be explained by the distinct habitat types and coastal change in the northern and southern sites. Fundamentally, examining these factors can help scientists and resource managers better understand how communities are structured and species diversity is maintained. Drivers of diversity change that are identified can be mitigated to ensure the protection of marine species and maintain the integrity of coastal habitats.

ACKNOWLEDGEMENTS

We are grateful to Fabiola Soong for supporting the students involved in this project, and the countless contributors of the Wild Fact Sheets. This research is supported by the National Research Foundation, Prime Minister's Office, Singapore, under its Marine Science R&D Programme (MSRDP-P03), as well as the Ministry of Education Academic Research Fund Tier 1 (R-154-000-A63-114). Field surveys were performed under a National Parks Board permit (NP/RP15-066).

LITERATURE CITED

- Allen GR & Werner TB (2002) Coral reef fish assessment in the "coral triangle" of southeastern Asia. *Environmental Biology of Fishes*, 65: 209–214.
- Bellwood DR, Renema W & Rosen BR (2012) Biodiversity hotspots, evolution and coral reef biogeography: a review. In: Gower D, Johnson K, Richardson J, Rosen B, Rüber L & Williams S (eds.) *Biotic Evolution and Environmental Change in Southeast Asia*. Cambridge University Press, Cambridge. Pp. 216–245.
- Bird M, Chua S, Fifield LK, Teh TS & Lai J (2004) Evolution of the Sungei Buloh–Kranji mangrove coast, Singapore. *Applied Geography*, 24: 181–198.
- Burke L, Selig E & Spalding M (2002) *Reefs at Risk in Southeast Asia*. World Resources Institute, Washington D.C., 72 pp.
- Chan IZW, Chang JJM, Huang D & Todd PA (2019) Colour pattern measurements successfully differentiate two cryptic Onchidiidae Rafinesque, 1815 species. *Marine Biodiversity*, 49: 1743–1750.
- Chan YKS, Toh TC & Huang D (2018) Distinct size and distribution patterns of the sand-sifting sea star, *Archaster typicus*, in an urbanised marine environment. *Zoological Studies*, 57: 28.
- Chang JJM, Ip YCA, Bauman AG & Huang D (2020) MinION-in-ARMS: Nanopore sequencing to expedite barcoding of specimen-rich macrofaunal samples from Autonomous Reef Monitoring Structures. *Frontiers in Marine Science*, in press. doi: 10.3389/fmars.2020.00448
- Chang JJM, Tay YC, Ang HP, Tun KPP, Chou LM, Meier R & Huang D (2018) Molecular and anatomical analyses reveal that *Peronia verruculata* (Gastropoda: Onchidiidae) is a cryptic species complex. *Contributions to Zoology*, 87: 149–165.
- Chim CK, Neo ML & Loh KS (2009) The status in Singapore of *Strombus (Dolomena) marginatus sowerbyorum* Visser & Man In't Veld, 2005 (Mollusca: Gastropoda: Strombidae). *Nature in Singapore*, 2: 379–384.
- Chou LM (1994) Marine environmental issues of Southeast Asia: state and development. *Hydrobiologia*, 285: 139–150.
- Chou LM (2006) Marine habitats in one of the world's busiest harbours. In: Wolanski E (ed.) *The Environment in Asia Pacific Harbours*. Springer, Dordrecht. Pp. 377–391.
- Chou LM, Huang D, Tan KS, Toh TC, Goh BPL & Tun K (2019) Singapore. In: Sheppard CRC (ed.) *World Seas: An Environmental Evaluation*. Volume II: The Indian Ocean to the Pacific. Academic Press, London. Pp. 539–558.
- Chow GSE, Chan YKS, Jain SS & Huang D (2019) Light limitation selects for depth generalists in urbanised reef coral communities. *Marine Environmental Research*, 147: 101–112.
- Chuang S-H (1961) *On Malayan Shores*. Muwa Shosa, Singapore, 225 pp.
- Chuang S-H (1977) Ecology of Singapore and Malayan coral reefs - preliminary classification. In: *Proceedings of the Third International Coral Reef Symposium, Volume 1*. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, pp. 55–61.
- Dana JD (1846) *United States Exploring Expedition during the years 1838–1842*. Volume 7. Zoophytes. C. Sherman, Philadelphia, 740 pp.
- Dickinson JL, Zuckerberg B & Bonter DN (2010) Citizen science as an ecological research tool: challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics*, 41: 149–172.
- Fautin DG, Tan SH & Tan R (2009) Sea anemones (Cnidaria: Actiniaria) of Singapore: abundant and well-known shallow-water species. *Raffles Bulletin of Zoology, Supplement 22*: 121–143.
- Friess DA, Phelps J, Leong RC, Lee WK, Wee AKS, Sivasothi N, Oh RRY & Webb EL (2012) Mandai mangrove, Singapore: lessons for the conservation of Southeast Asia's mangroves. *Raffles Bulletin of Zoology, Supplement 25*: 55–65.
- Glasby CJ, Lee Y-L & Hsueh P-W (2016) Marine Annelida (excluding clitellates and siboglinids) from the South China Sea. *Raffles Bulletin of Zoology, Supplement 34 (Part I)*: 178–234.
- Hilton MJ & Manning SS (1995) Conversion of coastal habitats in Singapore: indications of unsustainable development. *Environmental Conservation*, 22: 307–322. doi: 10.1017/S0376892900034883
- Hoeksema BW (2007) Delineation of the Indo-Malayan centre of maximum marine biodiversity: the Coral Triangle. In: Renema W (ed.) *Biogeography, Time, and Place: Distributions, Barriers, and Islands*. Topics in Geobiology. Springer Netherlands, Dordrecht. Pp. 117–178. doi: 10.1007/978-1-4020-6374-9_5

- Housing Development Board (1963) Annual Report. Housing Singapore Periodicals, Singapore. <http://eresources.nlb.gov.sg> (Accessed 01 Aug 2018).
- Huang D, Chou LM, Todd PA, Ang KH, Boon PY & Cheng L (2006a) Algal and invertebrate diversity of the intertidal zone at Labrador Nature Reserve, Singapore. *Malayan Nature Journal*, 59: 93–102.
- Huang D, Todd PA, Chou LM, Ang KH, Boon PY, Cheng L, Ling H & Lee W-J (2006b) Effects of shore height and visitor pressure on the diversity and distribution of four intertidal taxa at Labrador beach, Singapore. *Raffles Bulletin of Zoology*, 54: 477–484.
- Huang D, Tun KPP, Chou LM & Todd PA (2009) An inventory of zooxanthellate scleractinian corals in Singapore, including 33 new records. *Raffles Bulletin of Zoology, Supplement 22*: 69–80.
- Jaccard P (1901) Étude comparative de la distribution florale dans une portion des Alpes et des Jura. *Bulletin de la Société vaudoise des sciences naturelles*, 37: 547–579.
- Kobori H, Dickinson JL, Washitani I, Sakurai R, Amano T, Komatsu N, Kitamura W, Takagawa S, Koyama K, Ogawara T & Miller-Rushing AJ (2016) Citizen science: a new approach to advance ecology, education, and conservation. *Ecological Research*, 31: 1–19.
- Lai S, Loke LHL, Hilton MJ, Bouma TJ & Todd PA (2015) The effects of urbanisation on coastal habitats and the potential for ecological engineering: a Singapore case study. *Ocean and Coastal Management*, 103: 78–85.
- Lau CM, Kee-Alfian AA, Affendi YA, Hyde J, Chelliah A, Leong YS, Low YL, Megat Yusop PA, Leong VT, Mohd Halimi A, Mohd Shahir Y, Mohd Ramdhan R, Lim AG & Zainal NI (2019) Tracing coral reefs: a citizen science approach in mapping coral reefs to enhance marine park management strategies. *Frontiers in Marine Science*, 6: 539.
- Lee AC, Liao LM & Tan KS (2009a) New records of marine algae on artificial structures and intertidal flats in coastal waters of Singapore. *Raffles Bulletin of Zoology, Supplement 22*: 5–40.
- Lee AC, Tan KS & Sin TM (2009b) Intertidal assemblages on coastal defence structures in Singapore I: a faunal study. *Raffles Bulletin of Zoology, Supplement 22*: 237–254.
- Lee Q, Yaakub SM, Ng NK, Erfemeijer PLA & Todd PA (2012) The crab fauna of three seagrass meadows in Singapore: a pilot study. *Nature in Singapore*, 5: 363–368.
- Leray M & Knowlton N (2015) DNA barcoding and metabarcoding of standardized samples reveal patterns of marine benthic diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 112(7): 2076–2081.
- Low JKY (2013) More noteworthy fishes observed in the Singapore Straits. *Nature in Singapore*, 6: 31–37.
- Low JKY & Chou LM (1994) Coral reef fish communities in a sediment stressed environment. In: Fourth LIPI-JSPS Joint Seminar on Marine Science, Jakarta, pp. 91–99.
- Low JKY, Arshad A & Lim KH (1994) ASEAN mangroves as important centres of biodiversity and habitats for endangered species. In: Wilkinson CR (ed.) *Living Coastal Resources of Southeast Asia: Status and Management*. Report of the Consultative Forum, Third ASEAN-Australia Symposium on Living Coastal Resources. Chulalongkorn University, Bangkok, pp. 71–76.
- Low JKY, Tanzil JTI & Jaafar Z (2009) Some note-worthy fishes observed in the Singapore Straits. *Nature in Singapore*, 2: 77–82.
- Malaya Survey Department (1954) Map of Singapore (Scale: 1:63,360). Survey Department, Federation of Malaya, Malaya, 1 map.
- Milne Edwards H & Haime J (1849) Recherches sur les polypiers. Quatrième mémoire. Monographie des Astréides (I). Tribu II. Astréens (Astreinae). *Annales des Sciences Naturelles, Série 3, Zoologie*, 11: 233–312.
- Milne Edwards H & Haime J (1851) Recherches sur les polypiers. Sixième mémoire. Monographie des Fongides. *Annales des Sciences Naturelles, Série 3, Zoologie*, 15: 73–144.
- Morton B & Blackmore G (2001) South China Sea. *Marine Pollution Bulletin*, 42: 1236–1263.
- Murphy DH (1990) The natural history of insect herbivory on mangrove trees in and near Singapore. *Raffles Bulletin of Zoology*, 38(2): 119–203.
- Neo ML (2010) The taxonomic status of fig shells, with notes of *Ficus variegata* (Röding, 1798) (Mollusca: Gastropoda: Ficoidea: Ficidae). *Nature in Singapore*, 3: 117–123.
- Neo ML & Todd PA (2012a) Population density and genetic structures of the giant clams *Tridacna crocea* and *T. squamosa* on Singapore's reefs. *Aquatic Biology*, 14: 265–275.
- Neo ML & Todd PA (2012b) Giant clams (Mollusca: Bivalvia: Tridacninae) in Singapore: history, research and conservation. *Raffles Bulletin of Zoology, Supplement 25*: 67–78.
- Ng CSL, Jain SS, Nguyen NTH, Sam SQ, Kikuzawa YP, Chou LM & Huang D (2019) New genus and species record of reef coral *Micromussa amakusensis* in the southern South China Sea. *Marine Biodiversity Records*, 12: 17.
- Ng PKL & Low JKY (1994) Status of mangroves in Singapore: conservation beyond the year 2000. In: Wilkinson C, Sudara S & Chou LM (eds.) *Proceedings, Third ASEAN-Australia Symposium on Living Coastal Resources*. Volume 1: Status Reviews. Chulalongkorn University, Bangkok, pp. 229–232.
- Ng PKL & Sivasothi N (1999a) A Guide to the Mangroves of Singapore I. Singapore Science Centre, Singapore, 160 pp.
- Ng PKL & Sivasothi N (1999b) A Guide to the Mangroves of Singapore II. Singapore Science Centre, Singapore, 168 pp.
- Obura DO, Aeby G, Amornthammarong N, Appeltans W, Bax N, Bishop J, Brainard RE, Chan S, Fletcher P, Gordon TAC, Gramer L, Gudka M, Halas J, Hendee J, Hodgson G, Huang D, Jankulak M, Jones A, Kimura T, Levy J, Miloslavich P, Chou LM, Muller-Karger F, Osuka K, Samoily M, Simpson SD, Tun K & Wongbusarakum S (2019) Coral reef monitoring, reef assessment technologies, and ecosystem-based management. *Frontiers in Marine Science*, 6: 580.
- Oh RM, Neo ML, Yap NWL, Jain SS, Tan R, Chen CA & Huang D (2019) Citizen science meets integrated taxonomy to uncover the diversity and distribution of Corallimorpharia in Singapore. *Raffles Bulletin of Zoology*, 67: 306–321.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH & Wagner H (2013) *vegan: Community Ecology Package*. <http://vegan.r-forge.r-project.org> (Accessed 01 December 2018).
- Ong JY & Wong HP-S (2015) Report on sea cucumbers (Echinodermata: Holothuroidea) collected from the Johor Straits, Singapore. *Raffles Bulletin of Zoology, Supplement 31*: 273–391.
- Ong JY, Wong HP-S & O'Loughlin PM (2019) Two new tropical psolid sea cucumbers from the Strait of Johor, Singapore (Echinodermata: Holothuroidea) with a key to *Psolidium* species from the tropical East Indian-West Pacific region. *Raffles Bulletin of Zoology*, 67: 206–216.
- Phang VXH, Chou LM & Friess DA (2015) Ecosystem carbon stocks across a tropical intertidal habitat mosaic of mangrove forest, seagrass meadow, mudflat and sandbar. *Earth Surface Processes and Landforms*, 40: 1387–1400.
- Poquita-Du RC, Quek ZBR, Jain SS, Schmidt-Roach S, Tun K, Heery EC, Chou LM, Todd PA & Huang D (2019) Last species standing: loss of Pocilloporidae corals associated with coastal urbanization in a tropical city state. *Marine Biodiversity*, 49: 1727–1741.
- Quek RZB, Jain SS, Neo ML, Rouse GW & Huang D (2020) Transcriptome-based target-enrichment baits for stony corals

- (Cnidaria: Anthozoa: Scleractinia). *Molecular Ecology Resources*, 20: 807–818.
- Quek ZBR, Chang JJM, Ip YCA & Huang D (2019) Complete mitochondrial genome of the sea star *Archaster typicus* (Asteroidea: Archasteridae). *Mitochondrial DNA Part B*, 4: 3130–3132.
- Quek ZBR & Huang D (2019) Effects of missing data and data type on phylotranscriptomic analysis of stony corals (Cnidaria: Anthozoa: Scleractinia). *Molecular Phylogenetics and Evolution*, 134: 12–23.
- R Core Team (2013) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org> (Accessed 01 December 2018).
- Sheue C-R, Yong JWH & Yang Y-P (2005) The *Bruguiera* (Rhizophoraceae) species in the mangroves of Singapore, especially on the new record and the rediscovery. *Tawania*, 50: 251–260.
- Sin TM, Ang HP, Buurman J, Lee AC, Leong YL, Ooi SK, Steinberg P & Teo SL-M (2016) The urban marine environment of Singapore. *Regional Studies in Marine Science*, 8: 331–339.
- Tan KS, Koh KS & Goh L (2015) Taking stock of Singapore's marine life: the Comprehensive Marine Biodiversity Survey Johor Straits International Workshop 2012. *Raffles Bulletin of Zoology*, Supplement 31: 1–6.
- Tan KS, Acerbi E & Lauro FM (2016a) Marine habitats and biodiversity of Singapore's coastal waters: a review. *Regional Studies in Marine Science*, 8: 340–352.
- Tan KS, Koh KS, Ng JY & Goh L (2016b) The Comprehensive Marine Biodiversity Survey Singapore Strait International Workshop 2013. *Raffles Bulletin of Zoology*, Supplement 34 (Part I): 1–7.
- Tan LT & Chou LM (1993) Checklist of polychaete species from Singapore waters (Annelida). *Raffles Bulletin of Zoology*, 41(2): 279–295.
- Tan MK (2013) Orthoptera in the mangrove forests of Singapore. *Nature in Singapore*, 6: 289–300.
- Tan SK & Yeo RKH (2010) The intertidal molluscs of Pulau Semakau: preliminary results of "Project Semakau". *Nature in Singapore*, 3: 287–296.
- Tay JYL, Wong SKM, Chou LM & Todd PA (2018) Land reclamation and the consequent loss of marine habitats around the Ayer Islands, Singapore. *Nature in Singapore*, 11: 1–5.
- The Straits Times (1983) The great land reclamation at East Coast. *The Straits Times*, 21 November 1983, p. 7. <https://eresources.nlb.gov.sg/newspapers/Digitised/Article/straitstimes19831121.2.22> (Accessed 05 May 2020).
- Todd PA & Chou LM (2005) A tale of survival: Labrador Park, Singapore. *Coral Reefs*, 24: 391.
- Tulloch AIT & Szabo JK (2012) A behavioural ecology approach to understand volunteer surveying for citizen science datasets. *Emu*, 112: 313–325.
- van Strien AJ, van Swaay CAM & Termaat T (2013) Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *Journal of Applied Ecology*, 50: 1450–1458.
- Wainwright BJ, Ip YCA, Neo ML, Chang JJM, Gan CZ, Clark-Shen N, Huang D & Rao M (2018) DNA barcoding of traded shark fins, meat and mobulid gill plates in Singapore uncovers numerous threatened species. *Conservation Genetics*, 19: 1393–1399.
- Wells FE, Tan KS, Todd PA, Jaafar Z & Yeo DCJ (2019) A low number of introduced marine species in the tropics: a case study from Singapore. *Management of Biological Invasions*, 10: 23–45.
- Wong JSY, Chan YKS, Ng CSL, Tun KPP, Darling ES & Huang D (2018) Comparing patterns of taxonomic, functional and phylogenetic diversity in reef coral communities. *Coral Reefs*, 37: 737–750.
- Yaakub SM, Lim RLF, Lim WL & Todd PA (2013) The diversity and distribution of seagrass in Singapore. *Nature in Singapore*, 6: 105–111.
- Yaakub SM, McKenzie LJ, Erfteimeijer PLA, Bouma T & Todd PA (2014) Courage under fire: Seagrass persistence adjacent to a highly urbanised city–state. *Marine Pollution Bulletin*, 83(2): 417–424.
- Yap NWL, Fautin DG, Ramos DA & Tan R (2014) Sea anemones of Singapore: *Synpeachia temasek* new genus, new species, and redescription of *Metapeachia tropica* (Cnidaria: Actiniaria: Haloclavidae). *Proceedings of the Biological Society of Washington*, 127(3): 439–454.
- Yap NWL, Tan R, Yong CLX, Tan KS & Huang D (2019) Sea anemones (Cnidaria, Actiniaria) of Singapore: redescription and taxonomy of *Phymanthus pinnulatus* Martens in Klunzinger, 1877. *ZooKeys*, 840: 1–20.
- Yip ZT, Quek ZBR, Low JKY, Wilson B, Bauman AG, Chou LM, Todd PA & Huang D (2018) Diversity and phylogeny of *Sargassum* (Fucales, Phaeophyceae) in Singapore. *Phytotaxa*, 369: 200–210.