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Characterising Intertidal Ray Communities of North-East Australia

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Abstract

Tidal flat ecosystems are considered essential habitats for numerous elasmobranch species worldwide, yet regional-scale assessments of community composition and habitat use are largely lacking, particularly for batoids (rays). Aerial drone surveys were conducted at eight intertidal flats in North Queensland, Australia to better characterise patterns of species occurrence in tropical estuarine ($n=2$), marine beach ($n=3$), and offshore reef flat ($n=3$) environments. Between Sept 2020-Oct 2022, 155 video surveys were collected over repeat site visits, totalling 2,667 total ray observations. For each site, Machelef's species richness, community evenness, and species composition were calculated from the total observations. Nine species were encountered across three families (Dasyatidae, Aetobatidae, and Glaucostegidae), with most common species including Australian whipray *Himantura australis* ($n=1{,}295$), broad cowtail ray *Pastinachus ater* ($n=515$), mangrove whipray *Urogymnus granulatus* ($n=386$), giant shovelnose ray *Glaucostegus typus* ($n=233$), and pink whipray *Pateobatis fai* ($n=88$). Species richness among habitat types ranged from 1.34 to 3.16 and community evenness from 0.25 to 0.89. Estuarine sites contained highest relative abundances of *H. australis*, while beach flats supported more balanced mixed-species assemblages of *H. australis*, *G. typus*, and *P. ater*, and reef flats supported assemblages of *U. granulatus*, *P. ater*, *and P. fai*. This study offers one of the first multi-site comparisons of ray communities in North Queensland. Continuing these efforts and integrating with other methodologies will be valuable for elucidating species-habitat associations and drivers of community variability amidst increasing coastal change.

Keywords Batoid · Community ecology · Australia · Species composition · Drone survey · Intertidal

Introduction

Coastal species often depend on multiple habitats throughout their life cycles, with habitat quality and connectivity fundamentally shaping population dynamics across the seascape mosaic (Seitz et al., 2014). Essential habitats support a variety of ecological functions, serving as nurseries, foraging grounds, and refuges that enable population persistence, often for multiple species simultaneously (Sheaves et al., 2015). For mobile marine predators, identifying habitats that support populations through critical life stages remains a conservation priority, particularly where species face elevated extinction risk (Barnett et al., 2011; Speed et al., 2010).

The Indo-West Pacific region contains some of the most diverse elasmobranch assemblages on earth (Compagno et al., 2005; White et al., 2006). These populations also experience heightened risk of decline, primarily due to overfishing in regions such as Southeast Asia, where demand for fisheries resources is high and management capacity can be limited (Dulvy et al., 2021; Clark-Shen et al., 2023). In contrast, Australia is generally considered a 'lifeboat' for numerous elasmobranchs, representing regionally important strongholds for species that have been depleted elsewhere (Kyne et al., 2021; Simpfendorfer & Rigby, 2023). Tropical and subtropical waters along the Australian east coast are inhabited by several families of batoids (rays) including stingrays (Dasyatidae), eagle rays (Aetobatidae), wedgefish (Rhinidae), guitarfish (Rhinobatidae, Glaucostegidae), and

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sawfish (Pristidae), among others (Pierce et al., 2011; Taylor et al., 2011; Tobin et al., 2014; Yon et al., 2020).

While there is a general understanding of the geographical distributions, preferred habitats, and depth ranges of Indo-Pacific ray species (Last et al., 2016), less is known about which factors influence their distributions and finer-scale habitat use patterns (Cartamil et al., 2003; Vaudo & Heithaus, 2012). This gap is evident when evaluating species-habitat associations in complex coastal environments, where variation in substrate composition, vegetation, hydrology, and biotic communities can drive patterns at patchy microhabitat (m^2) scales (Franca et al., 2012; Hewitt et al., 2001; Wołowicz et al., 2007). Consequently, habitats that appear to have similar features may not be functionally equivalent or provide the same intrinsic value for species or communities (Bradley et al., 2019; Reis-Filho et al., 2019). Moreover, studying community structures and species-habitat associations while accounting for interactions among abiotic factors (e.g., salinity, temperature, substrate type), biotic factors (e.g., prey availability, predation risk), and individual-level characteristics (e.g., body size, physiological tolerances) remains important for identifying important habitats and understanding contextual drivers of community variability (Bradley et al., 2020; Lubitz et al., 2022).

Intertidal zones encompass a mosaic of coastal and estuarine habitats such as sand flats, mud flats, coral reefs, seagrasses, and mangroves (Kennish, 2002), of which unvegetated, soft bottom flats cover the greatest spatial area globally (Dhanjal-Adams et al., 2016; Murray et al., 2019). These habitats are under considerable pressure from coastal development, agricultural runoff, degraded water quality, and climate change impacts (Lotze et al., 2006; Murray et al., 2022; Rogers et al., 2023), prompting efforts to integrate knowledge of functional habitats into effective species management (Naiman & Latterell, 2005; Sheaves et al., 2015). Current estimates report that at least 45 species of rays use intertidal zones during one or more life stages, predominantly as juveniles (Leurs et al., 2023). While their dependence on such areas is linked to their abundant foraging opportunities, refuge from predators, and favourable abiotic conditions (Martins et al., 2018), relatively little information exists on which species and life stages are associated with intertidal habitats across the Australian tropics.

Historically, rays have been poorly sampled by conventional fishing gears including gillnets and bottom longlines, contributing to their underrepresentation in elasmobranch datasets outside of trawl surveys (White et al., 2013; Lemke & Simpfendorfer, 2023). Previous assessments of intertidal ray communities along the Queensland coast have primarily used capture methods (e.g., gillnets) (Adkins et al., 2016; Pierce et al., 2011; Tobin et al., 2014). More recently, remote sensing technologies have been adopted as an alternative to these gear-based approaches, enabling surveys of species presence and abundances in shallow waters (Colefax et al., 2019; Raoult et al., 2018; Schofield et al., 2019). Aerial drones are particularly suitable for collecting data across multi-site scales because they can cover large spatial areas with minimal effort while obtaining high-resolution data on species occurrences and distributions (Álvarez-González et al., 2023; Oleksyn et al., 2021). Additionally, drones can facilitate the observation of natural behaviour with minimal disturbance to the individual (Bourke et al., 2023; Crook et al., 2022; Schad & Fischer, 2023), allowing researchers to interpret fine-scale patterns in habitat use that are otherwise unattainable from capture or tagging studies.

In this study, we conducted aerial drone surveys at locations representing estuarine, marine beach flat, and offshore reef flat environments in North Queensland to summarise patterns in batoid community composition and habitat use throughout this region. We evaluate our findings both in terms of ecological patterns and the utility of drone-based surveys for assessing species composition in shallow coastal waters.

Methods

Study Sites

Eight sites were selected north and south of Townsville (-19.26639°, 146.8057°), North Queensland (Fig. 1) based on prior knowledge of ray occurrences from previous studies (e.g., Crook, 2020; Martins et al., 2020a, b), local expertise of the study authors, and where shallow depth (generally 1 m or less) and low turbidity conditions were attainable across repeated visits. While this targeted approach may have resulted in higher observation rates than randomly selected sites, this was necessary for characterising communities of mobile species that can occur at low densities, for which truly random sampling would be unlikely to yield sufficient observations and adequate statistical power (Pierce et al., 2011).

All sites experience semi-diurnal tidal regimes, with mean sea level ranging from 1.74 to 1.94 m. Differences in spring tidal height ranges were similar across sites, ranging from 2.03 to 2.19 m, with lesser extremes during neap tidal phases (0.58–0.78 m). Northernmost sites in the Hinchinbrook region and the Palm Islands experience the highest levels of rainfall during the wet season months from December to April (average annual rainfall 186 cm) compared to Cape Cleveland just south of Townsville (123 cm) or the Burdekin region farther south (110 cm). Shorelines of all sites were fringed by mangrove forests, generally of *Avicennia marina* and *Rhizophora stylosa*. Sites were

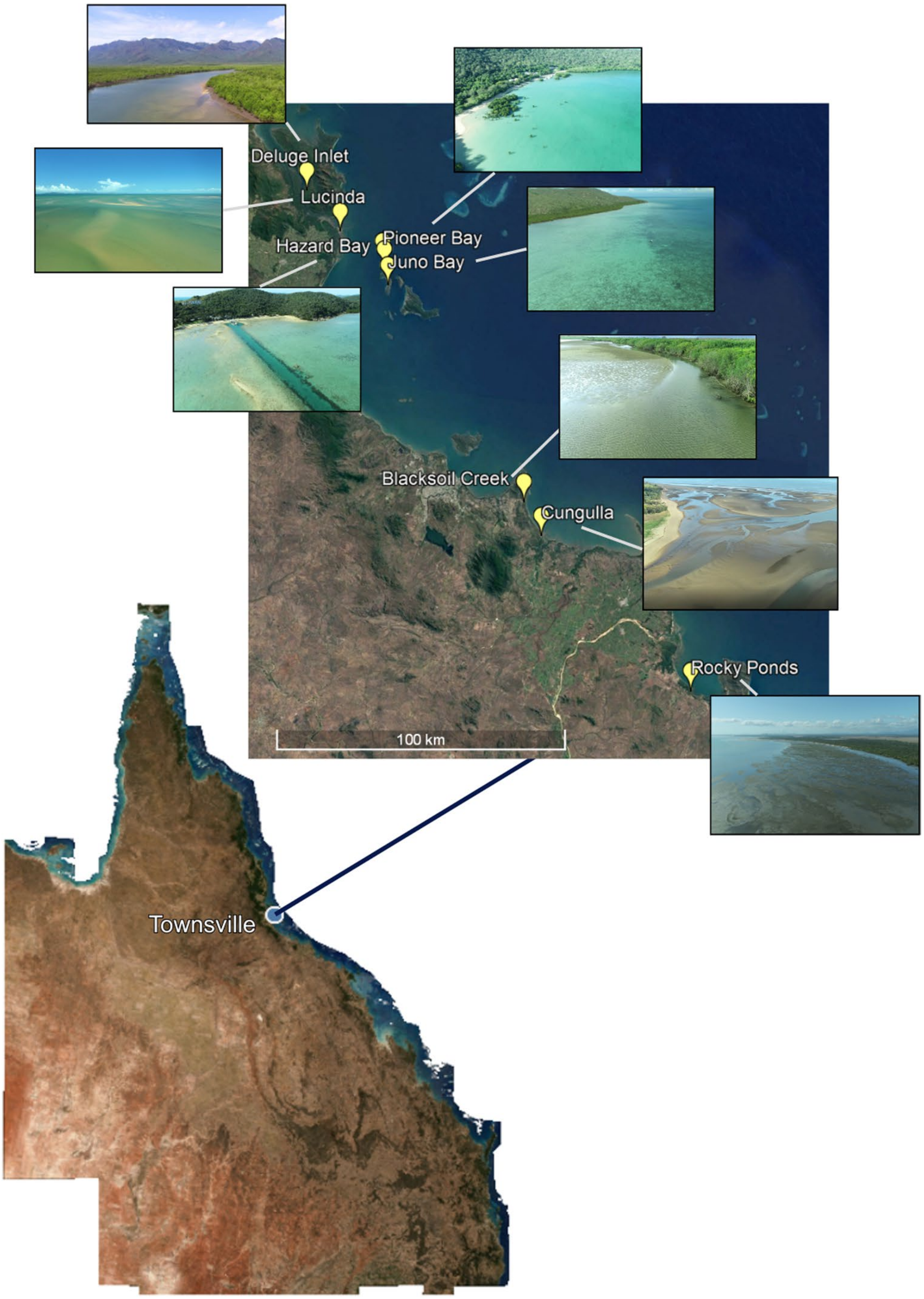

Fig. 1 Map of Queensland with inset showing the locations of eight intertidal flats where ray communities were surveyed north and south of Townsville, North Queensland. Basemap imagery from Google Earth: Image Landsat/Copernicus (December 2020)

classified into three types: estuary inlet (Blacksoil Creek, Deluge Inlet), marine beach flat (Cungulla, Lucinda Beach, and Rocky Ponds), or offshore reef flat (Pioneer Bay, Hazard Bay, Juno Bay) (Table 1). For all sites, sediment characteristics were assigned qualitatively based on observations made during site visits and knowledge from previous studies (Crook, 2020; Martins et al., 2022; Mattone & Sheaves, 2017; Sheaves et al., 2014).

Estuary inlets were characterised by steep mangrove banks and intertidal sand flats on the accreting banks, but sites differed in several aspects. Deluge Inlet receives high levels of freshwater runoff from Hinchinbrook Island, which flushes large amounts of sediments downstream and results in coarse sandy substrates within the channel (Sheaves et al., 2014). In contrast, intertidal flats in Blacksoil Creek are comprised of fine sand. At low tides, available habitat for marine life is restricted to the subtidal channels along the deeper edges, and sand flats along the accreting banks become periodically submerged during rising tides. Surveys were conducted upstream of the estuary mouths along the

Table 1 Characteristics of the eight sites surveyed using aerial drone transects from 2020–2022

Region	Site name	Site type	Substrate characteristics	Mangrove characteristics	Size of survey area (km^2)	Mean sea level (m)	Spring mean tidal range (m)	Neap mean tidal range (m)
Cape Cleveland	Blacksoil Creek	estuary inlet	sand flat, steep mud banks	on steep mud banks and along landward edges of sand flats	0.42	1.75	0.65–2.84	1.44–2.05
	Cungulla	beach flat	mud flat	along flat edges	1.43			
Hinchinbrook	Deluge Inlet	estuary inlet	sand flat, steep mud banks	on steep mud banks and along landward edges of sand flats	0.98	1.94	0.85–3.04	1.65–2.23
	Lucinda Beach	beach flat	sand flat	corner of sand flat	1.14			
Palm Islands	Pioneer Bay	reef flat	sand flat, coral rubble, dead micro atolls	on sand flat and edges	0.22	1.94	0.85–3.04	1.65–2.23
	Hazard Bay	reef flat	sand flat, coral rubble, dead micro atolls	on sand flat and edges	0.27			
	Juno Bay	reef flat	sand flat, coral rubble, dead micro atolls	on sand flat and edges	0.38			
Burdekin	Rocky Ponds	beach flat	sand flat, seagrass meadow	along flat edges	2.00	1.74	0.73–2.76	1.35–2.13

unvegetated sand flats and mangrove edges. One beach flat site was included in each region: Cungulla (Cape Cleveland), Lucinda Beach (Hinchinbrook), and Rocky Ponds (Burdekin). Cungulla and Lucinda Beach are primarily unvegetated areas with shallow tidal gradients extending seaward. Sediment composition at Lucinda Beach is primarily coarse sand with patches of fine sand and mud along the beach and mangrove forest (Crook, 2020), whereas Cungulla contains mostly mud and fine sand. Rocky Ponds differs by the presence of low-canopy seagrass species (*Zostera muelleri*, *Halophila ovalis*, and *Halodule uninervis*) that cover ~ 70% of the surveyed area (Carter et al., 2020) and is interspersed with unvegetated sandy patches. In the Palm Islands group, two reef flats were sampled at Orpheus Island (Pioneer Bay and Hazard Bay), and the other at neighbouring Fantome Island (Juno Bay). Reef flats at all sites consisted of sandy sediments near the shoreline and mangrove fringes, which were interspersed with greater amounts of coral and rocky rubble extending to the reef crests.

Transect Design

Drone video transects were collected from Sept 2020 to Oct 2022 using a DJI Phantom 4 drone and piloted with DJI Go 4 software. Transect flights were completed during daytime hours, most often in the early mornings between 06:00–11:00 when visibility was optimal (e.g., low wind, reduced glare). Due to opportunistic data collection and high variability in environmental factors (e.g., turbidity), the number of site visits and total transects varied among sites with a minimum of one transect and a maximum of nine transects completed per day. Where multiple transects were collected per day, consecutive flights over the same area were spaced at least one hour apart to minimise the likelihood of repeat ray detections. While repeat detections could not be eliminated entirely, this limitation was considered negligible, as ray communities were evaluated for this study using relative, rather than absolute measures of abundance (see *Analysis of community structure*).

Survey areas ranged from 0.22 to 2.0 km^2 depending on the size of the intertidal flat area and the steepness of the tidal elevation gradient, as well as accessibility to launching points for the drone. All drone surveys were completed within intertidal zones, apart from subtidal edges during low tides. Efforts were made to sample sites during more than one tidal period (low, rising, high, and ebb), although most survey effort took place during rising tides while rays were more likely feeding or moving to remain in shallow water as opposed to burying (Cartamil et al., 2003; Brinton & Curran, 2017). Using local tide charts, high and low tide periods were considered to span 1.5 h on either side of the slack tide, whereas the intervals of rising and falling water between these points were classified as flood and ebb tides, respectively. Given that intertidal areas would regularly become dry or water levels too deep for reliable identification to the substrate level, manual operations (rather than automated, repeated flights) were required. Areas were avoided where depths exceeded 1 m, as this obscured visibility.

For each transect, the drone followed a haphazard pathway over habitats that met the suitability criteria, and flights were continuous except for times when the pilot hovered briefly over a ray to confirm the species identity. Linear trajectories of all flight paths are displayed in Fig. 2. Data were extracted from the length and width of the video frame.

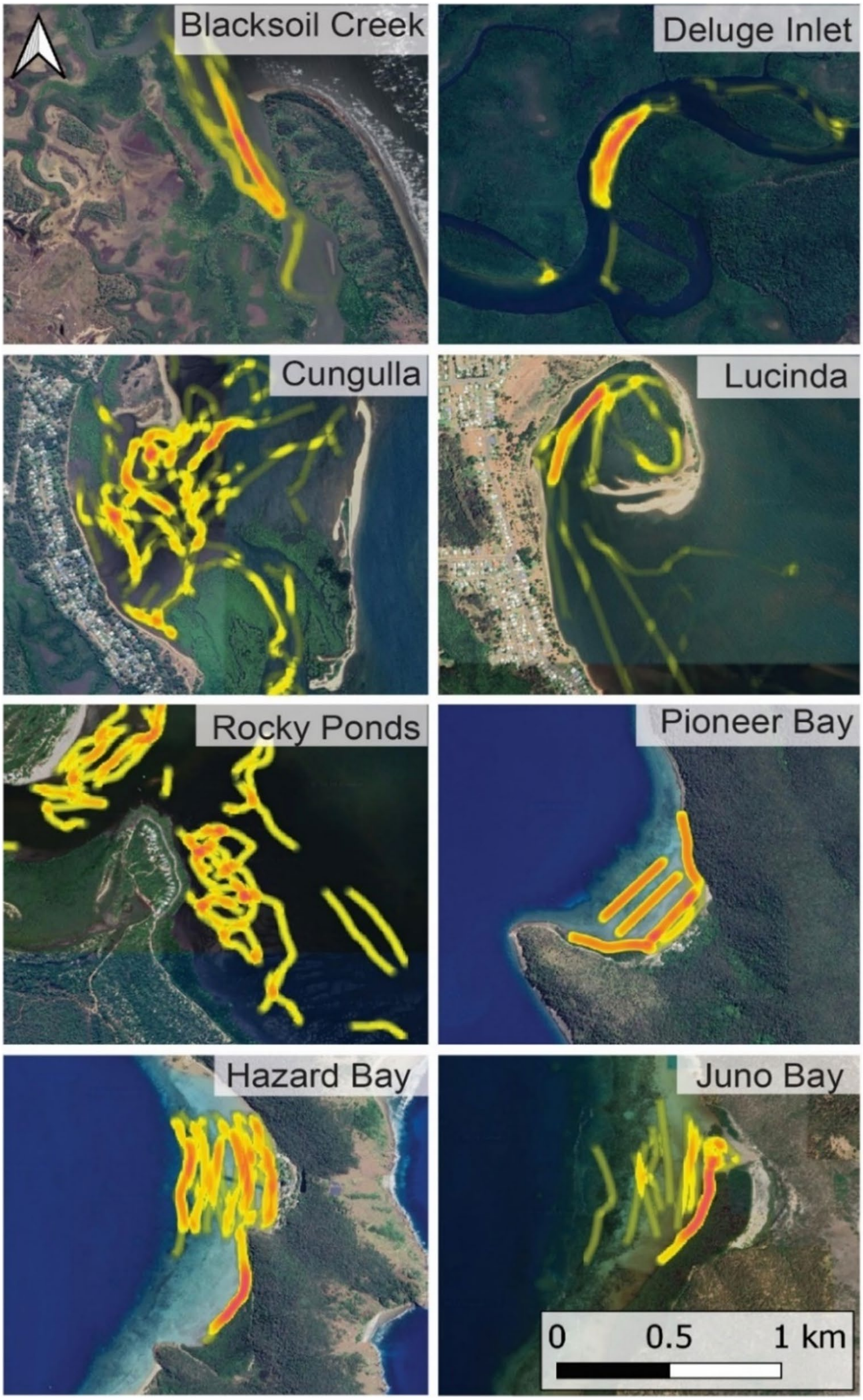

Fig. 2 Flight paths of all linear transects completed at each site. Darker orange line colours indicate areas that were covered more frequently, while fully transparent areas indicate areas that were not included in any flight path

The camera gimbal was angled 45–90° downward while recording video to reduce glare from the water surface, and flight speeds were maintained at <3 m s^{-1} to ensure objects remained in the video frame for sufficient time (McIvor et al., 2022). The duration of footage collected was subject to battery life of the drone and did not exceed twenty minutes per flight. Drone heights across transects varied since videos analysed here were collected for multiple purposes (e.g. ray identification, behavioural observations) and because visibility from a given height depended on daily fluctuations in cloud cover, wind, and glare. Drone heights used for analysis ranged from 5 to 30 m, encompassing the minimum height at which rays were detectable without being disturbed (Bourke et al., 2023) and the maximum height where species level identification was achievable. However, most flights were maintained between 10 and 20 m (*n* = 105), followed by 5–10 m (*n* = 36) and 20–30 m (*n* = 14).

Video Processing

All transect videos were viewed in VLC media player. Video segments were excluded where (1) the coverage area was dry or water too shallow for rays to be present or (2) turbidity, glare, or wave action resulted in poor visibility and rays could not be properly identified. All ray observations were identified to the species level. Where this was uncertain among similar taxa (Family Dasyatidae), these observations were categorised as *unknown dasyatid*. Locations of each sighting were approximated by matching the video time with the GPS coordinates of the overhead drone.

To approximate survey effort, transect areas (in km^2) were calculated by multiplying the transect distance in kilometres by the horizontal distance covered in the aerial footprint of the camera view. The latter was estimated by calculating the linear relationship between the drone's altitude and the ground sampling distance (Electronic supplemental material, Fig S1). To account for any changes in height throughout a transect, median drone heights were used to calculate ground sampling distance. For Blacksoil Creek and Deluge Inlet, transects primarily followed dry sand and mud bank edges due to limited visibility. These sites were excluded since deriving estimates using the camera's entire field of view (which generally included areas that were too deep or dry on either side of the edges) would overestimate the transect area. A summary of area-based metrics including transect area, total site coverage, and no. rays km^{-2}) are provided for each site in Table 2.

Analysis of Community Structure

Ray communities were summarised for each site using multiple metrics. Due to differences in survey effort among sites, species richness was calculated using Margalef's index (d) (Margalef, 1958), which effectively accounts for the number of species (s) relative to the number of individuals observed (N): (d = (s-1)/log(N) (Hyde et al., 2026). Community evenness was expressed using the Shannon Equitability Index (E), which incorporates species richness and the proportional abundance of each species (Magurran, 2003). Ranging from 0 to 1, lower values indicate that abundances are skewed towards one or more dominant species, while a value of 1 signifies that all species occurred in equal abundance. Species composition was then summarised for each site as percentages by dividing the total counts of each species by the total number of observations. Ray densities were not used to assess ray communities statistically, as transect-level estimates were largely variable and not considered to be directly comparable across habitats.

Results

Data were extracted from 155 drone video transects from Sept 2020 to Oct 2022. The greatest number of transects were collected at Blacksoil Creek (42 transects) and ranged from 5 to 27 transects for all other sites (Table 2). In total, 69 transects were collected during wet season months and 86 during the dry season months. Most transects were collected during rising tidal periods (*n* = 72), followed by low (*n* = 30), ebb, and high tides (*n* = 28 for each) (Table 2).

Nine ray species were identified across three families: Dasyatidae, Aetobatidae, and Glaucostegidae (Fig. 3). The most frequently encountered species were Australian whipray *H. australis* (*n* = 1,295), broad cowtail ray *Pastinachus ater* (*n* = 515), mangrove whipray *Urogymnus granulatus* (*n* = 386), giant shovelnose ray *Glaucostegus typus* (*n* = 233), and pink whipray *Pateobatis fai* (*n* = 88). Species encountered less frequently (< 5% of total species composition across all sites) included brown whipray *Maculabatis toshi* (*n* = 26), blue-spotted fantail ray *Taeniura lymma* (*n* = 18), spotted eagle ray *Aetobatus ocellatus* (*n* = 13), and porcupine ray *Urogymnus asperrimus* (*n* = 3). A visual overview of ray detections at each site is presented in Fig. 4. Species richness across sites ranged from 1.34 to 3.16 and community evenness (E) from 0.25 to 0.89, resulting in distinct clusters of sites (Fig. 5a). Sites positioned in the top right quadrant showed greater species richness with a more balanced species composition, whereas those positioned farther to the bottom left were indicative of communities dominated by fewer species.

The two estuarine sites showed dissimilarities in their community structures. Blacksoil Creek exhibited lower species richness and community evenness (d = 1.34, E = 0.25) relative to Deluge Inlet, which contained more balanced mixed-species assemblages (d = 1.93, E = 0.76) (Fig. 5a). The five ray species observed at Blacksoil Creek included four dasyatids: *H. australis*, *M. toshi*, *U. granulatus*, and *P. ater*, as well as *G. typus*. Notably, *H. australis* comprised 87.0% of the total observations with all other species contributing < 5% (Fig. 5b). At Deluge Inlet, *H. australis* remained the most commonly observed species (43.1% of total ray observations), but with greater contributions of *P.*

Table 2 Summary of drone video transects collected across the eight intertidal study sites from 2020–2022. Number of video transects and cumulative transect area coverage were used as approximations for sampling effort. Mean values are given in parentheses following the minimum-maximum ranges, whereas error estimates refer to the standard deviation of the mean

	Blacksoil Creek	Deluge Inlet	Cungulla	Lucinda Beach	Rocky Ponds	Pioneer Bay	Hazard Bay	Juno Bay
Coordinates	-19.300097, 147.043050	-18.414908, 146.218600	-19.398894, 147.115306	-18.533064, 146.338019	-19.819842, 147.669717	-18.612375, 146.488919	-18.634556, 146.498022	-18.683697, 146.516008
No. video transects	42	14	27	26	15	21	5	5
Dates ranges sampled	Sept 2020 – June 2022	Dec 2020 – Aug 2022	Dec 2020 – Apr 2022	May 2021 – Oct 2021	Feb 2022 – Sept 2022	Nov 2021 – Oct 2022	June 2022	June 2022
No. sampling days	13	6	8	5	4	11	1	1
No. transects with rays present	41	13	24	26	15	20	5	5
Season								
wet	14	2	25	0	15	13	0	0
dry	28	12	2	26	0	8	5	5
Tidal phase								
Low	13	5	0	0	5	5	1	1
Rising	16	7	18	14	5	9	1	2
High	8	2	0	10	1	3	1	1
Ebb	5	0	9	2	4	5	2	1
Drone height range								
Low (5–10 m)	10	6	14	6	0	0	0	0
Mid (11–20 m)	26	5	10	20	13	21	5	5
High (21–30 m)	6	3	3	0	2	0	0	0
Flight distance (m)	190–2240 (702)	285–2859 (929)	138–1653 (770)	320–3337 (1248)	239–911 (1955)	1642–5565 (3272)	1761–2414 (503)	1156–1724 (423.8)
Area per transect (km²)	.	.	2.9–51.2 (15.5 ± 11.3)	3.9–92.8 (26.8 ± 19.0)	4.5–44.6 (20.7 ± 10.7)	24.0–58.0 (43.5 ± 8.8)	53.3–75.3 (15.3 ± 4.4)	33.1–50.1 (12.3 ± 3.7)
Total sampling effort (sum of area across all transects (km²)	.	.	417.8	723.7	310.6	870.7	321.8	221.9
Number of rays per transect	0–53 (12.8 ± 11.0)	0–11 (4.3 ± 3.1)	0–33 (9.6 ± 8.1)	1–65 (17.2 ± 15.0)	1–24 (11.3 ± 6.6)	3–38 (15.8 ± 9.2)	10–33 (24.4 ± 9.4)	7–57 (23.2 ± 19.6)
Transect density (rays km^{-2})	.	.	0.0-3.5 (0.9 ± 0.9)	0.1–3.1 (0.8 ± 0.6)	0.1–1.7 (0.6 ± 0.2)	0.1–1.6 (0.3 ± 0.1)	0.2–0.51 (0.4 ± 0.1)	0.54–1.36 (0.6 ± 0.5)

ater (25.2%), and *U. granulatus* (23.6%). *Aetobatus ocellatus* and *G. typus* were also present in low abundance (<2.5% for both) (Fig. 5b).

Cungulla and Lucinda Beach were similar in terms of species richness (d = 2.07 and 2.22, respectively) and community evenness (E = 0.58 and 0.65), whereas Rocky Ponds exhibited the greatest species richness and a more even community structure (d = 3.16, E = 0.77) (Fig. 5a). Five species were identified at Cungulla, with species composition dominated by *H. australis* (53.1% of total ray observations), *P. ater* (28.5%) and *G. typus* (11.2%), with minor contributions by *A. ocellatus*, *U. granulatus*, and *U. asperrimus* (<1%) (Fig. 5b). While characterised by the same main species, species percentages for Lucinda Beach were more evenly distributed among *H. australis* (34.3% of total ray observations), *P. ater* (34.3%) and *G. typus* (26.7%). The most common species at Rocky Ponds were *P. ater* (30.8% of total ray observations), *G. typus* (26.6%), *U. granulatus* (21.3%) and *H. australis* (9.5%). Multiple other species including *P. fai*, *T. lymma*, *U. asperrimus*, and *A. ocellatus* were present in low abundance (<5% each) (Fig. 5b).

Species composition showed some variation among reef flats in the Palm Islands group. Seven species were present overall, with 4–5 species per site. Relative to survey effort, Hazard Bay had the highest species richness (d = 1.93), followed by Pioneer Bay (d = 1.61) and Juno Bay (d = 1.46) (Fig. 5a). Community evenness was similar between Hazard Bay and Pioneer Bay (E = 0.64 and 0.65, respectively) and highest for Juno Bay (E = 0.89). At all sites, *U. granulatus* dominated the species composition (45.7–53.0% of total ray observations), followed by *P. ater* (22.4–31.2%) and *P. fai* (8.2–21.6%) (Fig. 5b). *Glaucostegus typus* was observed multiple times at Juno Bay (8.6%) and was nearly or completely absent from other reef flats. Other species including *A. ocellatus*, *T. lymma*, and *H. australis* were present in low abundance (<3% for all).

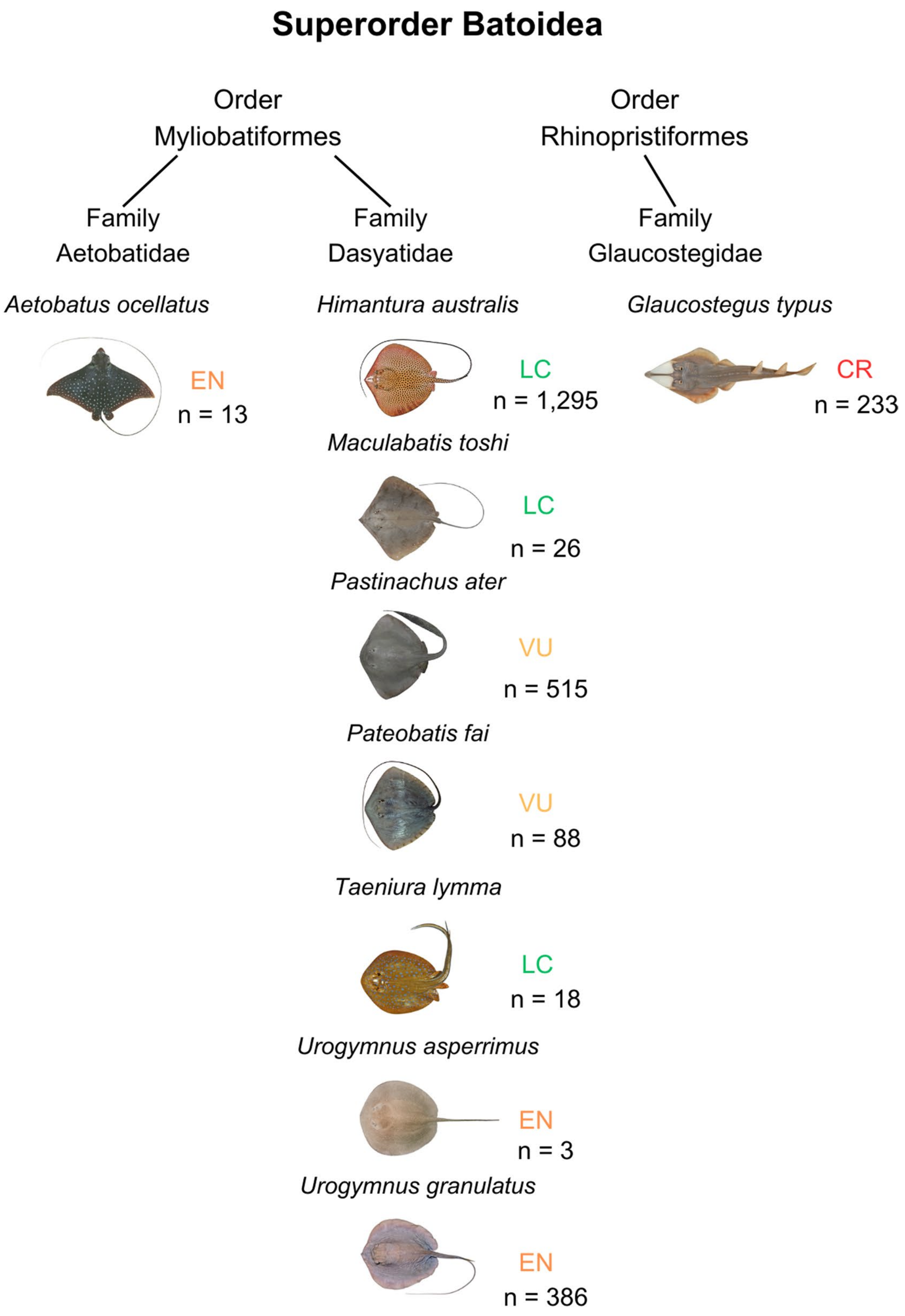

Fig. 3 A list of ray species identified within intertidal flats in North Queensland. Dasyatid species are stacked alphabetically. Abbreviations denote IUCN Red List conservation status: LC = Least Concern, VU = Vulnerable, EN = Endangered, CR = Critically Endangered. N denotes number of total observations across all sites. Graphics were sourced from the Australian National Fish Collection, CSIRO

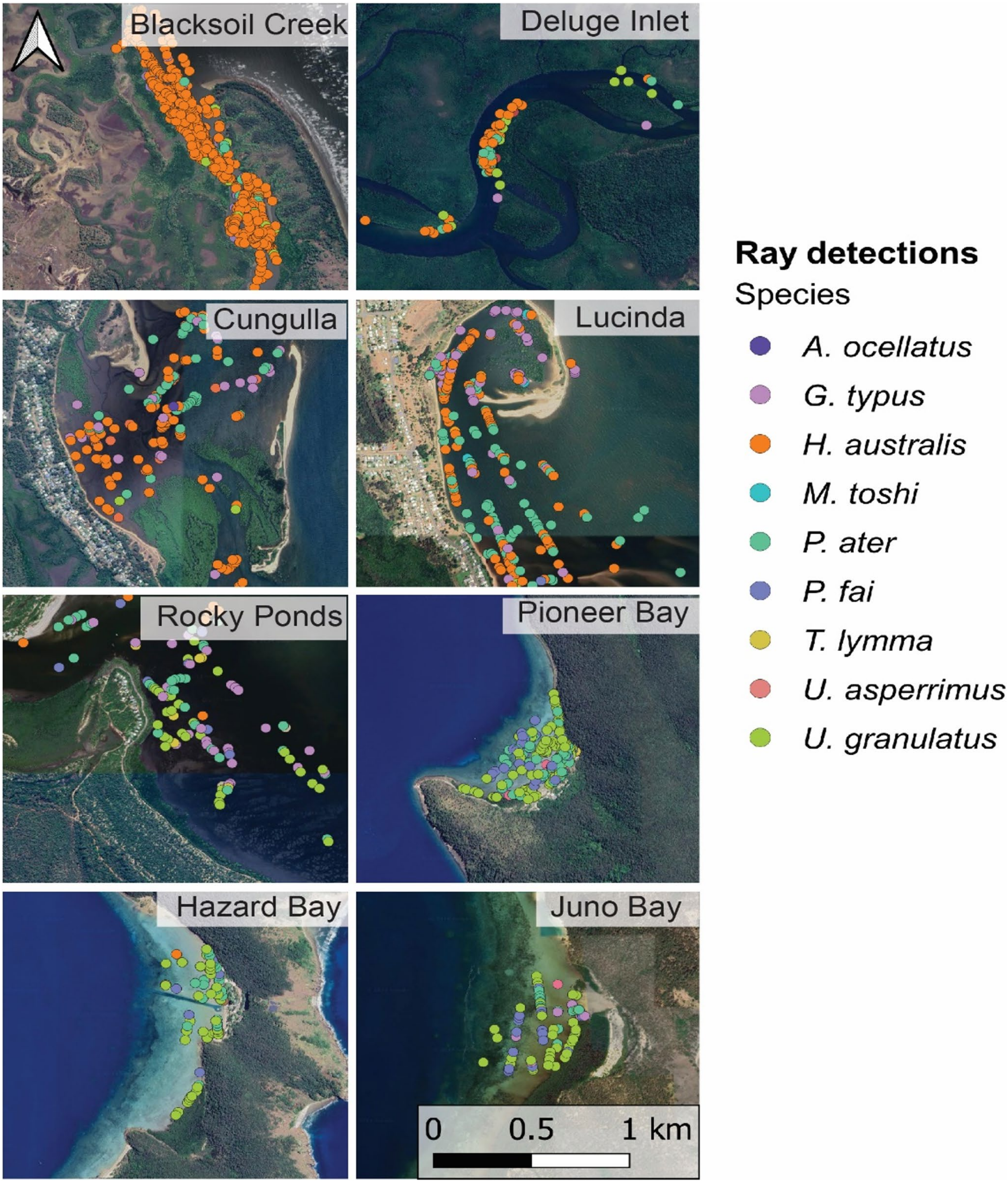

Fig. 4 Locations of all ray detections across the eight intertidal flats sampled using aerial drone surveys. Points are coloured by species

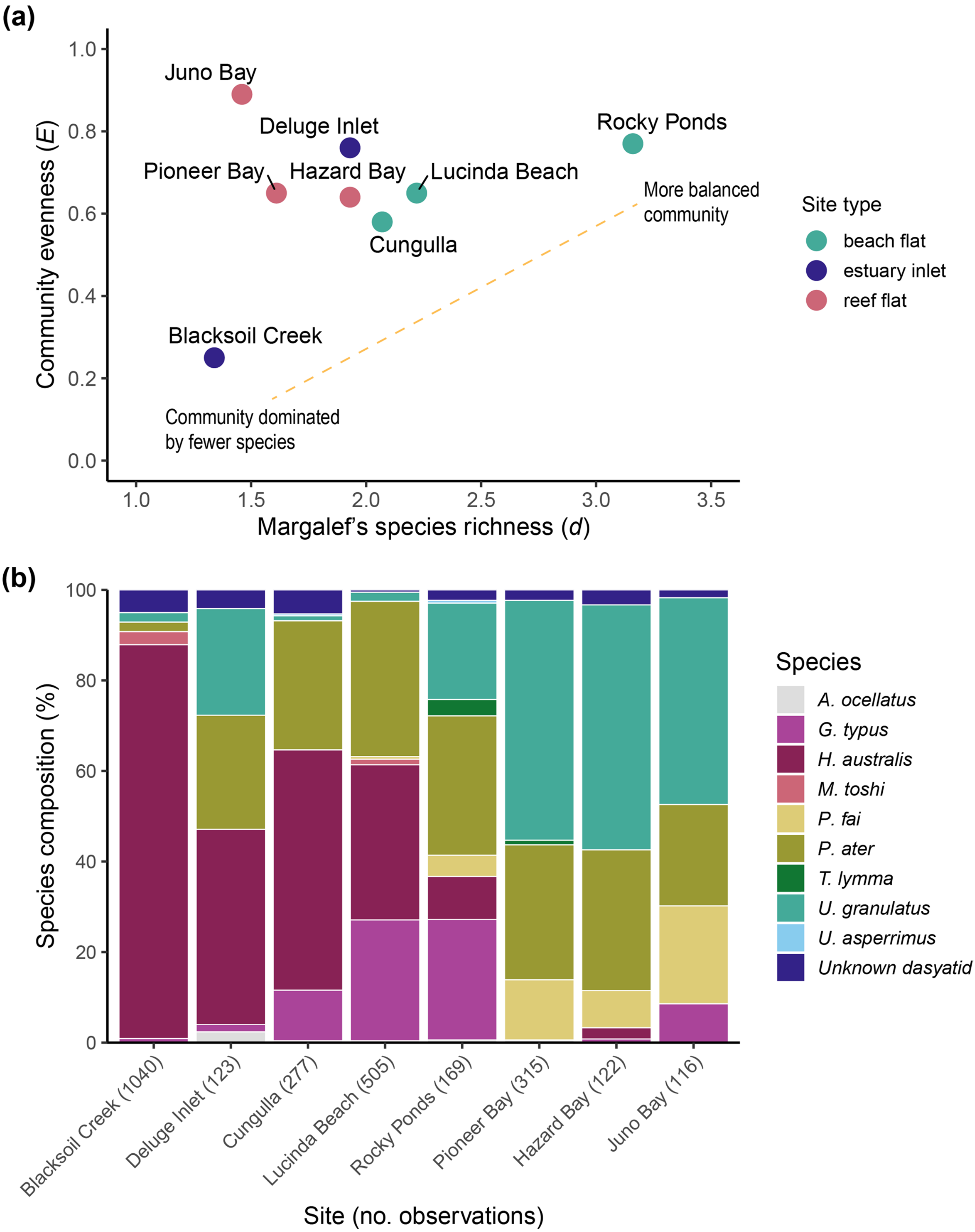

Fig. 5 (**a**) Site-level comparisons of ray community structures by Margalef's species richness (d) and community evenness (E). Each point represents one survey site with colour denoting the site type (either estuary inlet, marine beach flat, or offshore reef flat). (**b**) Species composition (%) for each site, with numbers in parentheses denoting the total number of ray observations

Discussion

Community Structure

Despite growing evidence supporting intertidal flats as essential habitats for numerous shark and ray species globally (Leurs et al., 2023), knowledge gaps persist regarding their community structures and species-habitat associations within these areas. Historically, these gaps have been compounded by methodological limitations with conventional sampling gear (White et al., 2013; Lemke & Simpfendorfer, 2023), although developments in drone technology have made surveying ray species more feasible in shallow-water environments (Oleksyn et al., 2021). Nevertheless, few studies have implemented drones to characterise ray community structures over broader regional scales. In this study, nine ray species across three families (Dasyatidae, Aetobatidae, and Glaucostegidae) were observed across estuary inlet, marine beach flat, and offshore reef flat habitats, representing just under half of at least twenty-one ray species that knowingly occur in intertidal habitats across North Queensland (Last et al., 2016) (Table 3). Notably, with information for many species being constrained by sparse occurrence records and uncertainties in true distributional ranges, species richness may be more widespread than what is currently documented, requiring further validations from field studies.

Ray communities were largely characterised by four co-occurring dasyatid species —*H. australis*, *P. ater*, *P. fai*, and *U. granulatus*—and the giant shovelnose ray *G. typus*. Moreover, differences in species composition among site types provided insights into community-level variability throughout the region. Other species including *A. ocellatus*, *T. lymma*, and *U. asperrimus* were also observed in the aerial transects, but low volume of observations precluded any detailed insight to patterns in habitat use. Although the International Union for Conservation of Nature (IUCN) has globally classified *P. ater*, *P. fai*, and *U. asperrimus* as Vulnerable, *U. granulatus* and *A. ocellatus* as Endangered, and *G. typus* as Critically Endangered, all species are listed as Least Concern in Australian waters and have sustainable populations (Simpfendorfer & Rigby, 2023).

The relative importance of estuaries to ray fauna remains poorly understood due to limited research on life history parameters, community structures, and habitat use of resident species (Cadwallader, 2020; Collins et al., 2007; Constance et al., 2024; Elston & Murray, 2024). This knowledge gap is particularly pronounced in tropical regions, where species distributions may be constrained by salinity tolerance and seasonal variations in freshwater inputs (Davis et al., 2012; Grant et al., 2019). Drone observations of rays at Blacksoil Creek were dominated by a single whipray species, *H. australis,* and other species contributed minimally to the overall assemblage, whereas at Deluge Inlet *P. ater*, *U. granulatus*, and *G. typus* comprised a greater portion. These findings were consistent with previous reports of each species entering estuaries (Last et al., 2016). Both *H. australis* and *P. ater* have been characterised as estuary-associated at least during one or more life stages (Constance et al., 2024), and estuaries are generally considered as important habitats for these species (Kyne et al., 2019; Rigby & Derrick, 2021; Sherman et al., 2021, 2024). Moreover, these findings confirmed the presence of understudied species including *M. toshi*, whose population sizes and life history traits remain largely unknown, although they are believed to prefer inshore habitats (Rigby & Pierce, 2016).

With greater sampling effort at Blacksoil Creek compared to Deluge Inlet (1040 observations versus 123 observations, respectively), some caution should be taken when comparing ray communities directly. However, differences in species compositions between inlets likely reflect differences in underlying habitat features and variable environmental conditions. For example, the position of Deluge Inlet on Hinchinbrook Island exposes it to substantial and near-continuous freshwater input from rainfall throughout the year, resulting in persistently lower salinity and a more extensive upstream salinity gradient (Sheaves et al., 2014). In contrast, the location of Blacksoil Creek in the dry tropics only exposes the estuary to substantial freshwater inputs during the wet season months, thus sustaining more marine conditions year-round. Overall, additional data that links species distributions and abundances with environmental parameters would be valuable for elucidating potential drivers of community-level variability.

Lucinda Beach and Cungulla were both largely unvegetated marine beach flats with some mangrove presence, and both shared similar mixed-species assemblages. Species compositions at each site were primarily comprised of *G. typus*, *H. australis*, and *P. ater*, which commonly co-occur in tidal flats throughout tropical and subtropical regions of Australia (Vaudo & Heithaus, 2009; Hyde et al., 2026). While we standardised species richness by total observations, raw species richness was nonetheless comparable to previous capture-based studies from sand and mud flats of Cape Cleveland Bay (Adkins et al., 2016; Tobin et al., 2014) and Moreton Bay (Pierce et al., 2011; Pillans et al., 2007), where six and nine ray species were identified, respectively. Using visual observation techniques, a recent study from eastern Moreton Bay in south-east Queensland reported similarly high species richness and diversity between mixed sand/mud habitats and intertidal mangroves, which exceeded that of inshore reefs or seagrass habitats (Hyde et al., 2026). Common species from Cungulla and Lucinda Beach, including *P. ater* and *G. typus*, were also abundant

Table 3 Batoid (ray) species with known associations with intertidal or shallow subtidal habitats along the north-eastern coast of Queensland (QLD), Australia. Parentheses following the scientific name denote any previous naming distinctions recognised for the species in the literature. Distribution ranges were listed based on descriptions by Last et al. 2016 and information available on the IUCN Red List database for each species; however, occurrences outside these ranges are possible. Species with exclusively southern distributions were excluded, as they would not expect to occur in the broader Townsville region. Known habitat types were adapted from the most recent IUCN Red List report available for each species at the time of publication

Family	Scientific name	Common name	Distribution across QLD east coast	Detected in current study	Known habitat types
Aetobatidae	*Aetobatus ocellatus (narinari)*	Spotted eagle ray	statewide	Y	Estuaries, subtidal (sandy), coral reef/lagoon, epipelagic
Dasyatidae					
	Himantura australis (uarnak)	Australian whipray	statewide	Y	Estuaries, subtidal (sandy, sandy/mud, muddy)
	Maculabatis astra	Black-spotted whipray	statewide	N	Subtidal (sandy, sandy/mud, muddy)
	Maculabatis toshi	Brown whipray	statewide	Y	Subtidal (sandy, sandy/mud, muddy), intertidal (mud flat, salt flat, mangrove)
	Neotrygon australiae (kuhlii)	Kuhl's maskray / Blue-spotted maskray	statewide	N	Subtidal (sandy, sandy/mud, muddy), coral reef (lagoon, inter-reef), intertidal (sandy shoreline/beach, mud flat, salt flat)
	Neotrygon trigonoides	Coral Sea maskray	statewide (northern extent Cooktown)	N	Subtidal (sandy, sandy/mud, muddy), coral reef (lagoon, inter-reef), intertidal (sandy shoreline/beach, mud flat, salt flat)
	Pastinachus ater (sephen)	Broad cowtail ray	statewide	Y	Estuaries, subtidal (sandy, sandy/mud), coral reef (lagoon), intertidal (mud flat, salt flat, mangrove)
	Pateobatis fai	Pink whipray	statewide	Y	Subtidal (sandy, sandy/mud, muddy), coral reef (inter-reef)
	Taeniura lymma	Blue-spotted fantail ray	statewide	Y	Coral reef, intertidal (mangrove)
	Urogymnus asperrimus	Porcupine ray	statewide	Y	Subtidal (sandy, sandy/mud), coral reef
	Urogymnus granulatus	Mangrove whipray	statewide	Y	Estuaries, subtidal (rocky, sandy, sandy/mud), seagrass, intertidal (rocky/sandy/pebbly shoreline/beach, mud flat, salt flat, mangrove)
Glaucostegidae	*Glaucostegus typus*	Giant shovelnose ray (guitarfish)	statewide	Y	Estuaries, subtidal (rock, rocky reefs, sandy, sandy/mud, muddy), coral reef (lagoon), intertidal (mud flat, salt flat)
Gymnuridae	*Gymnura australis*	Australian butterfly ray	statewide	N	Subtidal (sandy, sandy/mud, muddy)
Myliobatidae	*Aetomylaeus vespertilio*	Ornate eagle ray	statewide	N	Pelagic, estuaries, subtidal (sandy), seagrass, epipelagic
Pristidae					
	Anoxypristis cuspidata	Narrow sawfish	N QLD -southern extent Rockhampton	N	Pelagic, estuaries, subtidal sand/mud, coral reef/lagoon, seagrass, sandy shoreline, intertidal mud and salt flat, mangrove
	Pristis clavata	Dwarf sawfish	statewide	N	Wetlands, estuaries, subtidal (sandy, sandy/mud, muddy) coral reef (inter-reef), seagrass, intertidal (mud flat, salt flat, mangrove)
	Pristis pristis	Largetooth sawfish	N QLD - southern extent Cairns	N	Wetlands, estuaries, subtidal (sandy, sandy/mud, muddy), seagrass, intertidal (mud flat, salt flat, mangrove)
	Pristis zijsron	Green sawfish	statewide	N	Subtidal (rock/rocky reefs, sandy, sandy/mud, muddy), coral reef (inter-reef), seagrass, intertidal (sandy shoreline/beach, mud flat, salt flat, mangrove)
Rhinidae	*Rhynchobatus australiae*	Bottlenose wedgefish	statewide	N	Estuaries, subtidal (rock/rocky reefs, sandy, sandy/mud, muddy), coral reef
Trygonorrhinidae	*Aptychotrema rostrata*	Eastern shovelnose ray	S QLD - northern extent Townsville	N	Estuaries, subtidal (rock/rocky reefs, sandy, muddy), seagrass, intertidal (mud flat, salt flat)
Rhinopteridae	*Rhinoptera neglecta*	Australian cownose ray	statewide	N	Pelagic, intertidal (mud flat, salt flat)

in diverse sand habitats of Moreton Bay. However, this site also contained greater numbers of coral-associated species including *P. fai* and Coral Sea maskray *Neotrygon trigonoides* (Last et al., 2016) (potentially reflecting the closer proximity of these sites to inshore reefs), as well as the estuary stingray *Hemitrygon fluviorum*, whose distributional range is not known to extend north into the wet tropics.

Rocky Ponds supported the highest species richness across all sites surveyed in this study. The presence of low-canopy seagrass species on the sandy tidal flat may have created additional habitat complexity that contributed to this observation. While inclusion of seagrass at a single site precluded any definitive comparisons with our other survey sites, other studies have reported high diversity of sharks and ray taxa in seagrass and seagrass-adjacent habitats (Peterson & Grubbs, 2020; Young & Carlson, 2024); however, elasmobranch diversity does not appear to be universally higher compared to unvegetated habitats (Hyde et al., 2026). In Australia, the most comprehensive assessments of ray communities from nearshore areas with seagrass are from Shark Bay, Western Australia (Heithaus et al., 2013; Vaudo & Heithaus, 2009, 2013; White & Potter, 2004), which is broadly characterised by persistent, meadow-forming species (i.e., *Posidonia australis* and *Amphibolis antarctica*). The shared occurrences of various ray species between Shark Bay, Moreton Bay, and Rocky Ponds including *P. ater*, *H. australis*, *P. fai*, *G. typus*, and *A. ocellatus* coincide with their broad distributional ranges and shared habitat preferences across the Australian tropics and subtropics. Notably, *U. granulatus* is the only species we observed for which seagrass has been listed by the IUCN as a habitat of major importance (Sherman et al., 2024). While there is increasing evidence to support direct uses of seagrass (e.g., foraging) by all main species (Vaudo & Heithaus, 2011; Elston et al., 2020), functional dependencies between seagrass and associated species remain poorly investigated.

Offshore reef flats contained similar ray assemblages, which is unsurprising given their close geographic proximity and shared habitat characteristics. The most common species we observed were *P. ater*, *U. granulatus* and *P. fai*, which are largely ubiquitous across tropical and subtropical reef environments (Chin et al., 2010; Last et al., 2016; Yon et al., 2020). High abundances of *P. ater* and *U. granulatus* have been similarly documented in other geographic contexts, including intertidal flats surrounding St. Joseph's Atoll in the Seychelles (Elston et al., 2020, 2021), indicating a broader affinity to these habitats. At Pioneer Bay, the consistent presence of juvenile *U. granulatus* and *P. ater* is likely driven by their high fidelity to the reef flat over consecutive tidal cycles (Davy et al., 2015; Martins et al., 2020a, b), which is mirrored at Hazard Bay and Juno Bay. Lesser occurrences of *P. fai* could indicate they use deeper subtidal areas, rather than being restricted to the shallow intertidal zones that were accessible to drones (Vaudo & Heithaus, 2009). Notably, reef flats contained low abundances of *H. australis* and *G. typus*, despite these species being more prevalent in tidal beach flats and estuaries, which may indicate greater preferences for unvegetated soft bottom habitats over direct associations with the coral reef structure (Cerutti-Pereyra et al., 2013; Freeman, 2019; Gaskins et al., 2020; O'Shea et al., 2012). Notably, while ray assemblages have been described for offshore island and reef atolls in other geographic regions (i.e., Pikitch et al., 2005; Elston et al., 2021), comparable published data of ray assemblages from similar contexts across the Great Barrier Reef World Heritage Area remain scarce.

The occurrence of shared species across different locations is likely driven by shared physical characteristics, whereas connectivity between different habitat patches may further facilitate movement across mosaic microhabitats and increase overlap in species assemblages at these scales (Boström et al., 2018; Skilleter et al., 2017). Soft bottom flats surrounded by intertidal mangroves provide shared functional benefits to multiple species, particularly as batoid nurseries (Martins et al., 2018; Leurs et al., 2023). While body sizes were not estimated directly from the drone surveys, previous catches of *H. australis*, *P. ater*, M. *toshi*, and *G. typus* at Blacksoil Creek and Lucinda Beach comprised exclusively young-of-year and juvenile size classes (Myers et al., 2025a, b). Furthermore, prior research in Pioneer Bay further supports this site to be a nursery for *P. ater* and *U. granulatus* (Martins et al., 2022), with neighbouring reef flats throughout the Palm Islands likely fulfilling similar functions.

Nursery benefits, such as foraging opportunities and reduced risk of predation, further underpin use of intertidal flats. Benthic rays generally exhibit strong dietary preferences for benthic invertebrates (Flowers et al., 2021), which can occur in peak abundances in the lower intertidal zone (Sheaves et al., 2016). This pattern was consistent with the high densities and spatial clustering of feeding pits observed across drone imagery at multiple sites. Differences in foraging habits could also influence habitat use at these scales. Trophic ecology studies conducted at Lucinda Beach, Blacksoil Creek, and Pioneer Bay similarly demonstrate inter-specific dietary niche separation (Myers et al., 2025b; Martins et al., 2022), which is common across various species and habitat contexts (O'Shea et al., 2013; Pardo et al., 2015). Drone tracking studies also provide emerging opportunities to study unique foraging behaviours among species in these habitats (Crook et al., 2022; Myers et al., 2026). Although resource partitioning and spatio-temporal variability in prey may contribute to the fine-scale patterns of abundance observed, the mechanisms underlying these relationships (including their interactions with abiotic factors) require further investigation.

Limitations

While drones were effective for species-level identification of ray fauna, we acknowledge the limitations of drone use in this study as this pertains to visibility and detectability of species across different environments (Butcher et al., 2021; Colefax et al., 2019; Raoult et al., 2020). Coastal areas in North Queensland experience high turbidity that constrain suitable survey conditions and tidal fluctuations that greatly influence habitat accessibility, which required manual flight path planning to collect usable data for each habitat. Although data collection was restricted to areas where the substrate was visible, buried rays could have been overlooked against bare sand substrates, as could small-bodied and more plainly coloured species (such as *M. toshi*). Cryptic species such as *T. lymma* that typically shelter under coral structures may also be underrepresented in observation on reef flats, and some instances of species misidentification may have occurred between the morphologically similar species *H. australis* and *P. fai.* Thus, integrating drone-based surveys with capture-based approaches may remain beneficial for characterising community structures while minimising biases associated with any single method, particularly where visibility constraints exist.

Conclusions

This study provided one of the first multi-site comparisons of ray communities across intertidal flats in north-east Queensland using drone surveys. Expanding such efforts across different habitat contexts will further validate these findings and enable more robust comparisons of species-habitat relationships. Moreover, observational methods may offer greater insights into spatial habitat partitioning over fine spatial scales. For instance, while *H. australis*, *P. ater*, and *G. typus* were common ray species at Lucinda Beach, *H. australis* and *P. ater* have been shown to forage over different microhabitats, possibly due to differences in spatial prey availability (Myers et al., 2025b; Crook et al., 2022). Pairing drones with other complementary methodologies (i.e., animal tracking, trophic and behavioural studies) will therefore be highly useful for identifying underlying drivers of community variability.

Lastly, as this study focused on relatively pristine areas within a regional scope, future research incorporating sites with varying degrees of development or degradation would provide further insights into population vulnerabilities and resilience. Moreover, given robust fisheries management in Australia and its recognition as a lifeboat nation for Indo-Pacific elasmobranch species, documentation of natural community structures in the absence of major threats will provide informative baselines for protecting species with elevated extinction risk in other regions (e.g., giant shovelnose ray) (Simpfendorfer & Rigby, 2023). Ultimately, understanding the ecological roles of intertidal flats for dependent species will have lasting implications for informing globally effective management strategies amidst accelerating coastal change.

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Declarations

Ethics approval Animal ethics approvals for drone research were conducted under James Cook University approval #A2810.

Competing interests The authors have no other competing interests to declare which are relevant to this article.

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