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Abstract

Geography plays an important role in the distribution of plants on islands. This is in part because of the diversity of places and associated environmental conditions in which the islands are located, but also because of how islands are positioned with respect to one another. This relative positioning enters explicitly into island biogeographical character and can be expressed through spatial models. Over the past 20 years, spatial techniques for the empirical analysis of biological datasets have been increasingly applied to investigate biogeographical phenomena, particularly toward a better understanding of spatially structured underlying causative factors. These might include dispersal and competition, as well as environmental and historical influences. This study investigates patterns in the number of plant species occurring on 43 islands of the Great Barrier Reef (GBR) at three different geographical sectors (whole GBR, northern GBR, and southern GBR). Measures of spatial autocorrelation are calculated to explore the relationship between the diversity of plant populations on a given island and those on neighbouring islands. The relationship between the number of island plant species and local geographical context (latitude, longitude, distance from mainland, island area, island length, depth of surrounding GBR lagoon floor and island isolation) is investigated using three different regression models (ordinary least squares, spatially lagged and spatial error). Findings indicate that the southern islands exhibit the strongest spatial autocorrelation of plant species number between islands. In this sector, geographical context also explained the highest proportion of observed plant species numbers. The distribution of the number of plant species and their autocorrelation characteristics indicate metapopulation dynamics that could be a response to the variable sea-level history of these islands through the Holocene. This controls the time that plant communities have had to reach and maintain a dynamic equilibrium with their local environmental setting. Consistent higher performance of spatial as opposed to classic regression models highlighted the importance of interactions between plant communities on neighbouring islands, providing a persuasive case for explicitly building geography into studies of island plant communities.

Keywords

reef, barrier, great, cays, sand, southern, northern, plants, australia, number, geographical, affecting, factors, investigation

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A GEOGRAPHICAL INVESTIGATION OF FACTORS AFFECTING THE NUMBER OF PLANTS ON NORTHERN AND SOUTHERN SAND CAYS OF THE GREAT BARRIER REEF, AUSTRALIA

SARAH M. HAMYLTON¹

ABSTRACT

Geography plays an important role in the distribution of plants on islands. This is in part because of the diversity of places and associated environmental conditions in which the islands are located, but also because of how islands are positioned with respect to one another. This relative positioning enters explicitly into island biogeographical character and can be expressed through spatial models. Over the past 20 years, spatial techniques for the empirical analysis of biological datasets have been increasingly applied to investigate biogeographical phenomena, particularly toward a better understanding of spatially structured underlying causative factors. These might include dispersal and competition, as well as environmental and historical influences. This study investigates patterns in the number of plant species occurring on 43 islands of the Great Barrier Reef (GBR) at three different geographical sectors (whole GBR, northern GBR, and southern GBR). Measures of spatial autocorrelation are calculated to explore the relationship between the diversity of plant populations on a given island and those on neighbouring islands. The relationship between the number of island plant species and local geographical context (latitude, longitude, distance from mainland, island area, island length, depth of surrounding GBR lagoon floor and island isolation) is investigated using three different regression models (ordinary least squares, spatially lagged and spatial error). Findings indicate that the southern islands exhibit the strongest spatial autocorrelation of plant species number between islands. In this sector, geographical context also explained the highest proportion of observed plant species numbers. The distribution of the number of plant species and their autocorrelation characteristics indicate metapopulation dynamics that could be a response to the variable sea-level history of these islands through the Holocene. This controls the time that plant communities have had to reach and maintain a dynamic equilibrium with their local environmental setting. Consistent higher performance of spatial as opposed to classic regression models highlighted the importance of interactions between plant communities on neighbouring islands, providing a persuasive case for explicitly building geography into studies of island plant communities.

INTRODUCTION

Geography plays an important role in the distribution of plants on islands. This fact was well known to David Stoddart, who spent much of his time on the Great Barrier Reef collecting and identifying plants to collate species lists by island, to enable a comparative analysis of their distribution. His efforts provide a foundation for the present study, which was inspired by a visit to David at his home in Oxford Street in April 2013. During that visit, David and I discussed plant biogeography on the Great Barrier Reef. Then he coaxed me down to his infamous basement, where he handed me his northern Great Barrier Reef plant species lists and uttered the words “*we really ought to do something with these, can you help, Sarah?*” This study combines those lists with records provided by Harold Heatwole for the southern Great Barrier Reef to investigate geographical factors affecting plants on the islands of the Great Barrier Reef.

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The sand cays of the Great Barrier Reef (GBR) have formed through the build-up of carbonate materials (coral sand or shingle, molluscs, calcareous algae and foraminifera) over the last 4000 years (Hopley, 2008). Vegetation on these islands has played an important role in island evolution because root systems stabilise carbonate sedimentary deposits and thereby contribute to island structural integrity (Heatwole, 2011). From a biogeographical perspective, the plant populations on islands are the product of overwater dispersal, which itself is strongly shaped by the distance from neighbouring coastlines and differing sea level histories, which determine island age and associated availability of a platform for colonisation.

Mueller-Dombois and Fosberg (2013) consider the spatial distribution of island vegetation to be a function of six factors: geographical location (geology and geomorphology), climate (local and regional), disturbance, flora, access of plants or disseminules to a specific locality and the ecological functional role of plants making up a community. Geography plays an important role across each of these factors in two distinct ways. These can be explored empirically by treating island geographical locations as ‘place’ or as ‘space’, herein referred to as geographical place and geographical space. A treatment of island geographical place draws on the diversity of places in which the islands are found to vary the associated environmental conditions that drive their biogeographical character, thus emphasising the importance of *place* as context for plant species found on islands. The Great Barrier Reef stretches more than 2000 km from north to south, supporting a diverse array of over a thousand islands. Each of these islands is situated in a unique set of local environmental conditions characterised by a combination of exposure to incident waves, wash-over, storms, tidal range and cyclone frequency (Hamylton and Puotinen, 2015; Heatwole, 2011). In turn, these influence the compositional features of islands including their sedimentary characteristics and habitat diversity that also shape plant populations (Buckley, 1985). In a survey of 603 plant species, Heatwole (1991) used statistical regression to investigate the effects of geographical place on the plant communities of both continental and cay islands on the Great Barrier Reef, finding a large proportion of the observed variation in the number of island plant species to be a function of island area and height.

An alternative view of geographical space emphasizes how islands are located with respect to one another, and how this relative positioning enters explicitly into their biogeographical character. Biological variability might arise from interactions between the islands that are a function of those spatial relationships. Such variability might be expressed through measurements such as distance, gradient and neighbourhood context. The identity of the plants on a given island depends on the composition of plant communities on neighbouring islands from which colonizing propagules may have travelled. Thus, the relationship between these two islands induces an effect in both locations that is not purely a consequence of the inherent properties of the two respective immediate locations. This is because the processes that influence island plant biogeography, including dispersal and plant species interactions, are also spatially structured. The tendency for organisms to disperse away from a site of origin is determined by the both structure of the environment and the method by which an organism disperses (Kinlan and Gaines, 2003). Plants such as mangroves shed their reproductive propagules at a relatively small size to disperse through a large and complex fluid environment (Stoddart, 1980). This provides potential for wide transport through a marine environment structured by ocean frontal systems and currents (Kinlan and Gaines, 2003), vertical stratification of the water column (Longhurst, 2010) and changes in substrate and bathymetry, particularly the presence of a suitable substrate for colonisation (i.e., the presence of a shallow island on a submerged shelf lagoon) (Gaines et al., 2007). Furthermore, once plants have colonised an island, they may aggregate because of resource availability, predator or competitor avoidance, mating behaviour, limited dispersal and advection, symbiosis, parasitism and disease in ways that give rise to spatial patterning (Robinson et al., 2011). The biological distribution of plants therefore emerges as a phenomenon driven by these two different conceptualisations of geographical place and space, which operate at a hierarchy of scales from the immediate neighbourhood up to regional scales along and across the reef shelf. It is therefore useful to explore the distribution of plants on islands using spatial techniques that draw explicitly on their position in the sense of both geographical place and space.

Spatial autocorrelation (known more broadly as spatial dependency) refers to the correlation of a single characteristic (e.g., plant species number) as a function of its position in geographic space

(Hamylton, 2017). Positive spatial autocorrelation occurs when characteristics at proximate locations are more closely related than their distant counterparts, producing a clumped pattern (in contrast, negative autocorrelation can arise when characteristics close together are more unlike due to competition, producing a dispersed pattern). It is well known that plant communities of nearby islands tend to be similar because they are influenced by comparable spatially structured processes and neighbourhood interactions. But to what extent are these shaped by the distinct roles of geographical place and space? If a model is constructed to explain plant species number based on environmental correlates and the performance of that model improves with the incorporation of a spatial lag or error term that compares each island to its neighbouring islands, the implication is that neighbourhood interactions play an important role. Indeed, the extent to which the performance of the model changes with the incorporation of the spatial terms is indicative of the relative influence of geographical place and space. Allied developments in fields such as geographical information science have opened up the discipline of biogeography to the statistical exploration of population datasets through enquiry in which the location of information is explicitly incorporated (Haining, 2003).

This study investigates spatial patterns in the plant diversity of 43 islands (encompassing 613 species), across both the northern and southern sectors of the Great Barrier Reef. First, spatial autocorrelation is measured and interrogated for three geographic sectors (whole barrier reef, northern islands, southern islands) in order to explore spatial dependency between the diversity of plant populations on a given island and those on neighbouring islands. Second, for the same sectors, the relationship between the number of plant species supported by each island and the local geographical context (latitude, longitude, distance from mainland, island area, island length, depth of surrounding GBR lagoon floor and island isolation) is investigated using three different regression models (ordinary least squares, spatially lagged and spatial error). These models are compared to elucidate the relative influence of geographical place and space on the number of plant species supported by each island.

MATERIALS AND METHODS

Study Sites

The Great Barrier Reef (GBR) is the largest reef province in the world, containing over 1000 islands, including 350 coral cays (Hopley et al., 2007). Stretching over 15° of latitude and with reef islands extending from the mainland to the shelf edge, the GBR spans a considerable diversity of local climatic conditions. Tropical cyclones form between November and April, with a pronounced late-summer peak when sea conditions are warmest (Harmelin-Vivien, 1994). The eastern boundary of the GBR intercepts swell waves generated across the Pacific Ocean and Coral Sea and islands are subject to smaller trade wind-generated waves within the GBR lagoon. Varying sea level histories along and across the continental shelf have resulted in a range of time windows over which islands have accumulated since the most recent post glacial transgression. Hydro-isostatic adjustment of the shelf to sea-level rise has meant that the sea attained its present level later at the outer reef (Lambeck et al., 2010) suggesting that the distance of an island from the mainland can be treated as a proxy for the time-range over which islands have developed. Accordingly, islands closer to the coastline may have had longer to accumulate (Hopley, 2008). Shallow drilling, U-series and radiocarbon dating evidence indicates that the underlying reef platforms grew on top of antecedent surfaces over the last 8000 years (Marshall and Davies, 1982, Woodroffe and Webster, 2014, Larcombe et al., 1995). It has been suggested that this was followed by a series of evolutionary sequences that lead to island formation through sediment infill into reef top depressions (see island evolutionary classification proposed by Hopley et al., 2007). Open water microatolls indicate a potential mid-Holocene sea-level oscillation of 1–1.5m above present sea level across the inner northern GBR suggesting a minor fall in sea level since then (Chappell, 1983). Subsequent researchers have inferred oscillations (for a review, see Lewis et al., 2013) and it is likely that significant variation in glacio- and hydro-isostatic adjustments across these regions has given rise to a geographically heterogeneous pattern

of relative sea-level history. This has undoubtedly influenced the character of the islands that represent the end-point of these geomorphic transitional sequences.

Biogeographical work on the plants of the sand cays across the GBR can largely be classified as:

1. descriptive visual surveys and collections made with the aim of establishing distributions, regional schemes, boundaries and disjunctions;
2. studies applied to individual islands with the aim of characterising change within the context of biogeographical processes such as dispersal and drift or human influence; and,
3. larger scale studies that make phytogeographic observations across island groups, where possible drawing on regional empirical observations to infer reasonable explanations for patterns observed.

In relation to the first class, notable floristic collections include those made by Joseph Banks from the *Endeavour*, Robert Brown from Matthew Flinders' expedition on the *Investigator*, MacGillivray (1852), Steers (1938) and work in the southern islands summarised by (Chaloupka and Domm, 1985). Studies that fall into the second class have focussed on individual islands, particularly those southern islands easily accessible from the mainland that have been subject to more intense anthropogenic influence. From the Capricorn-Bunker group, these include Lady Elliot Island (Batianoff, 1998), Masthead Island (Batianoff, 1999), Heron Island (Smith and Heatwole, 1985), Wilson, Northwest, Hoskyn and Fairfax Islands (Cribb, 1965; Cribb, 1969; Cribb, 1972; Cribb, 1986). Regional studies that fall into the third class propose explanations of the distribution of the island flora of GBR and include the aforementioned modelling study by Heatwole (1991) and a comparative study by Stoddart and Fosberg (1991), who noted the marked difference between the floras of the southern and northern islands. The former were Indo-Pacific or pantropical in character and the latter were distinctively Australian, comprising a 'North Queensland element'. They proposed that the distinction between woodland flora of clear Australian affinity in the north and littoral flora of Indo-Pacific composition in the south reflected different dispersal mechanisms.

Table 1 summarises the broad classes of plant associations observed on sand cays of the GBR. Island vegetation types include tropical trees and shrubs, mangroves and seagrasses, which perform important ecosystem services such as sediment stabilisation, nutrient processing, shoreline protection, and provide habitat and nursery grounds (Duke and Larkum, 2008). On stable, older cays, mature soils, perhaps with guano deposits, have had time to form a climax woodland vegetation. For example, *Pisonia grandis*, often exists in association with phosphatic soils enriched by guano, although a highly dynamic environment may mean that all stages of a vegetational succession are present on a single island (Hopley et al., 2007). Commonly occurring plants span littoral and herbaceous species, shrubs, vines and trees, such as *Pisonia grandis*, *Tournefortia argentia*, *Casuarina equisetifolia* and *Pandanus tectorius* (Heatwole, 1987).

Survey Data

The islands of the Capricorn-Bunker group, including Lady Elliot, Lady Musgrave, Heron, One Tree Island and Fairfax were surveyed by the author during three fieldtrips in December 2012, June 2013 and May 2014. Additional plant survey data were provided for 15 southern and central islands of the present study by Harold Heatwole (Heatwole, 1991) and David Stoddart provided plant survey information for a further 28 islands that were mapped on the *1973 Royal Society and Universities of Queensland Expedition to the Northern Great Barrier Reef* (Stoddart, 1978). Individual species lists are available from the Queensland Herbarium, Brisbane for the southern islands and have been published in the *Atoll Research Bulletin* for the northern islands (Fosberg and Stoddart, 1991). All surveys were undertaken during expeditions that were of a comparable length (three to four weeks), which permitted collections to be made for approximately one day per island, thus controlling for variations in collection effort. All species encountered were recorded in the survey plant lists, with the following inclusions and exclusions noted for introduced species (pers. comm): *Lantana spp.* (included), *Cocos nucifera* (included), *Opuntia spp.* (excluded). For the two islands that were re-surveyed by the author (Lady Musgrave and Heron Island) the early species lists were adopted for the analysis, as in both cases these were more extensive.

Measurement of Spatial Autocorrelation in Number of Plants Observed at Three Geographic Sectors

Three areas of observation were defined for the purpose of this study. These were determined by the geographical scope of the field campaigns in which the plant surveys were undertaken and the observed difference between the floras of the northern and southern islands of the GBR (Stoddart and Fosberg, 1991). Each island was treated as a single data point of known location supporting a known number of plants. Firstly, an analysis of all islands surveyed was undertaken spanning the length of the entire Great Barrier Reef (n=43; Figure 1). This region was then subdivided into a northern sector encompassing the islands surveyed on the expedition to the northern GBR, i.e., those north of Low Isles

Table 1. Common plant associations on sand cays of the Great Barrier Reef (summarised from Stoddart and Fosberg, 1991).

Plant associations	Description
Initial plant colonisation on sand cays	Young communities of vascular plants, including coconut seedlings, grasses and creepers. Often subject to disturbance, such as cyclone damage or overtopping by swash at high tide.
Beach-crest scrub and herbaceous vegetation with trees	Variable in composition, dependent on island size. Beach-crest vegetation continuous cover of herbs and grasses, scattered shrubs inland and scattered low trees
Scrub and succulent sward of rock platforms	Lithified windward rubble and shingle platforms that support low, extensive monospecific scrub regularly submerged at high tide (<i>Aegialitis annulata</i> or <i>Avicennia marina</i>), succulent mats on the rock surface frequently wetted by spray, vegetative outposts on inner, upper shingle ridges
Scrub and herbaceous cover of windward shingle ramparts	Ridged shingle ramparts inside conglomerate platforms with vegetation becoming more continuous and dense on older, inner ridges and merging into inland scrub
<i>Pemphis</i> scrub and scrub-woodland	<i>Pemphis acidula</i> (northern islands) in exposed situations on rocky and thin shingle substrates, including on the seaward shores of sand cays, on the inner margin of upper conglomerate windward platforms and at the boundary of sand cay / mangrove swamps of low wooded islands
Mixed scrub and herbaceous vegetation	An open mosaic of low shrubs, herbs, vines and grasses on sandy substrates in the interiors of smaller, lower cays.
Scrub woodland	As above, with less diverse ground cover and taller trees
Woodland of sand and sand-shingle islands	Dense, close canopy woodland found on larger islands. Dominated by <i>Pisonia</i> in the southern islands, with interior phosphate rock. Also support shrubs, but limited herbs and grasses due to canopy density
Mangroves	Mangroves are only present in the northern islands, with common types defined as shrubs (<i>Avicennia marina</i> , <i>Aegialitis annulata</i>), thicket (<i>Ceriops</i> , <i>Osbornia</i>) and woodland (<i>Rhizophora mucronata</i> var. <i>stylosa</i>)
Human-modified vegetation	Anthropogenic grasslands, <i>Agave</i> thicket, removal of natural woodland and scrub and introduction of exotic trees and decorative plants / weeds. Selective encouragement of useful trees by Aboriginal communities.

(n= 28), and a southern sector encompassing the Swains and the Capricorn –Bunker Group surveyed by Harold Heatwole, several of which were later re-surveyed by the author (n = 15, excluding two islands from the central reef) (Heatwole, 1987). To measure spatial dependency in the plant populations of the islands surveyed, spatial autocorrelation calculated as the univariate Moran's *I* statistic for the number of plants observed at each island on the datasets corresponding to each spatial extent. The overall Moran's *I* metric indicated the strength of spatial autocorrelation across the island groups at each spatial extent, on a scale of -1 (negative spatial dependency) to +1 (positive spatial dependency). The significance of the resulting statistic was tested using a permutation approach in which a reference distribution was calculated 999 times for spatially random layouts with the same data values to construct a reference distribution

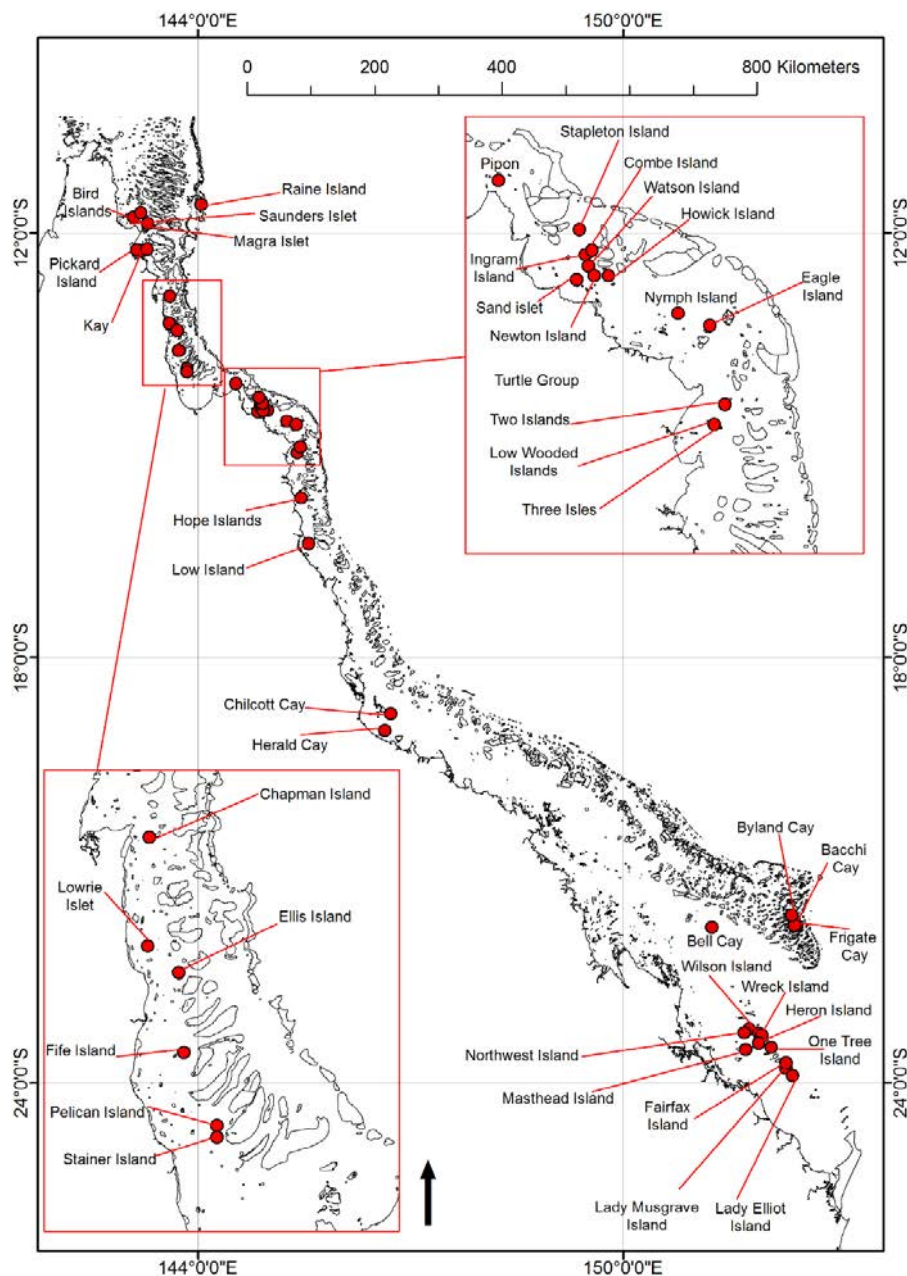


Figure 1. The 43 reef islands for which plant surveys were undertaken.

against which the pseudo significance level is computed as the ratio of the number of statistics for the randomly generated datasets that are equal to or exceed the observed statistic to the number of permutations used (Anselin, 1996). To compute this statistic, a spatial weights file was constructed in which a threshold Euclidean distance of 6.11 km was defined, which was the minimum distance necessary for all islands to have at least one neighbour. Any islands falling inside this distance threshold were defined as a neighbour and assigned a weight of one within the spatial weights matrix.

Moran's I values were then presented in the form of a Moran scatter plot (Anselin, 1995). The scatter plot was constructed by plotting the number of plant species observed at each island against the spatially lagged weighted average of the variable (number of plant species observed) at neighbouring islands. Variables were normalised into standard deviations, such that graph quadrants corresponded to four types of spatial autocorrelation: *high-high* (upper right), *low-low* (lower left), for positive spatial autocorrelation, and *high-low* (lower right) and *low-high* (upper left), for negative spatial autocorrelation. Thus, the scatter plots indicated the presence of spatial dependency by virtue of the quadrants in which island data points fell, with points falling in the upper right and lower left quadrants indicating positive spatial autocorrelation, and points falling in the upper left and lower right quadrants indicating negative spatial autocorrelation.

Assessing the Relationship Between the Number of Species of Plants Observed on Each Island and the Local Geographical Context

Local geographical context was characterised through the following variables: latitude, longitude, distance from mainland, island area, island length, depth of surrounding GBR lagoon floor and island isolation (see Table 2).

Table 2. Variables employed to represent the biogeographical context of each island surveyed.

Biogeographical context variable (range of values)	Description
Latitude (11.59°S to 24.11°S)	<i>y-coordinate of island centroid</i> : A gradient of variation in climate (rainfall, temperature), tidal range and cyclone frequency
Longitude 143.13°E to 152.45°E	<i>x-coordinate of island centroid</i> : A gradient of exposure to oceanic swell
Distance to mainland 4 km to 190 km	<i>Euclidean distance to Queensland coastline</i> : A proxy for the length of time available for islands to develop since the postglacial marine transgression
Island area 0.00045km ² to 0.3 km ²	<i>Area of island / km²</i> : An indicator of island structural integrity, degree of washover, carrying capacity and probability of plant colonisation through interception of propagules
Island length 0.2 km to 1 km	<i>Length of longest island axis / km</i> : An indicator of island structural integrity, degree of washover, carrying capacity and probability of plant colonisation through interception of propagules
Depth of surrounding lagoon floor -75m to -13m	<i>Average depth of surrounding lagoon floor</i> : A proxy for the length of time available for islands to develop since the postglacial marine transgression
Island isolation	<i>Land area within 6.11 km radius of island</i> : An indicator of the potential for supply of propagules from neighbouring land masses and their associated plant communities.

The depth of the surrounding GBR lagoon floor (excluding the reef platform) was chosen as an indication of the vertical distance that each reef would have had to grow to catch up with sea-level, which in turn indicates the length of time over which islands have been able to form. This value was determined by extracting the average value from a surrounding subset of a digital elevation model of the Great Barrier Reef (Beaman, 2010). Local statistics were computed by applying a buffer to each island centroid to define a circle of radius 2.11 km around each island, for which the digital elevation model was retained. This distance was the range defined by a semivariogram and corresponded to the distance beyond which the number of plant species no longer influenced each other due to spatial dependence (Hamylton, 2013). Within each buffer zone, a mask was applied to remove shallow values from reef platforms and the average of the bathymetric values associated with the remaining deeper GBR lagoon floor pixels from the digital elevation model in each zone was calculated for each island. The variable of island isolation was included to account for adjacent reservoirs of potential colonising plants (Stoddart and Fosberg, 1991). Island isolation was calculated as the amount of land falling within a distance of the aforementioned range of 6.11 km of each island. This was defined by creating buffer of 6.11 km around the vector dataset representing each island shoreline. The buffer dataset was then intersected with the overall islands dataset that represented bodies of emergent land across the broader GBR region.

Prior to the implementation of the regression models, variables were checked to ensure that the following assumptions of regression were met: adequate number of islands per independent variable, absence of outliers, linearity of association between the dependent and each independent variable, absence of multi-collinearity, normality, heteroscedasticity and constant variance of residuals and the independence of observations.

Three different regression models were developed using the open source software GeoDa. These assessed the relationship of the observed number of species of plants on each island to the local geographical context: ordinary least squares, spatially lagged and spatial error (Hamylton, 2017). These were applied to a range of geographical areas, including across the entire GBR ($n=45$), within the northern islands ($n=28$) and within the southern islands ($n=13$). The second and third models introduced a spatially explicit term to the regression equation that either took the form of a spatially lagged dependent variable (sometimes referred to as an 'autoregressive' term), or a modelled estimate of the spatial error. This explicitly accounted for the relative location of each island by taking information from neighbouring islands into account. Where positive spatial autocorrelation is present, the development of non-spatial models of plant species numbers across the islands increases the likelihood of a Type I error through artificial inflation of goodness of fit measures because some of the effect due to spatial interaction would have been allocated to the existing covariates. By developing models with a spatially dependent structure, such as the spatial lag model or spatial error model, this can be addressed through re-specification to incorporate a neighbourhood context effect operating through the response variable itself. In the case of a spatial lag model, if the dependent variable is the number of plant species on the islands, the spatially lagged term represented the average number of plant species calculated for all neighbouring islands falling within a distance of 6.11 km (i.e. the spatial lag) from the island for which the number of plants was to be modelled. In the case of the spatially lagged response variable, this is akin to stating that the number of plant species surveyed at a given island might itself be a function of those surveyed at neighbouring islands. The spatial error model took an alternative approach that subdivided the error term arising from a standard OLS regression model into spatially structured unexplained and unexplained components. The former component was then modelled by incorporating the error at a neighbouring location as a regression variable, thereby enabling it to be accounted for without the cause necessarily being known.

All three regression models explored the effects of geographical place on the number of island plant species by empirically exploring their relationship to a range of geographical context variables. The two spatial regressions further accounted for information from neighbouring islands. This did not require information on any additional covariates, rather, they utilised the location information of each island to construct a geographically weighted term to express the number of plant species as a function of their relative position.

RESULTS

Figure 2 illustrates the univariate Moran scatter plot of spatial autocorrelation for each of the three spatial extents studied. Most island data points fell within the lower left and upper right quadrants, indicating positive spatial autocorrelation. This was corroborated by Moran's *I* statistics of moderate strength at two of the spatial extents corresponding to all islands and in the northern sector (Moran's *I* of 0.48 and 0.35 respectively), and of higher strength between the southern islands (Moran's *I* of 0.71).

Spatial models consistently performed better at explaining variation in the number of plant species observed on each island than the ordinary least squares model at every geographical extent of application (Table 3).

Table 3. Diagnostics of the three different types of regression of the relationship between the number of plant species and local biogeographical context of each sand cay. Values in brackets indicate z-scores for ordinary least squares models and t-statistics for spatial models.

Variables: β coefficient (z-score or t-statistic)								
	Lat	Long	Distance to main-land	Island Area	Island length	Lagoon depth	Island isolation	R² (p-value)
All islands (n=45)								
Ordinary least squares	-2.04 (-2.91)	-0.12 (-1.33)	-17.50 (-4.20)	-5.83 (-1.50)	51.28 (0.90)	0.32 (1.93)	50.45 (3.78)	0.41 (p<0.02)
Spatially lagged	-1.32 (-1.98)	-0.07 (-0.91)	-12.16 (-2.70)	-4.77 (-1.39)	51.92 (1.03)	0.20 (1.30)	41.54 (2.31)	0.51 (p<0.03)
Spatial error	-1.62 (-2.04)	-0.08 (-0.75)	-16.72 (-3.41)	-4.49 (-1.31)	52.16 (1.06)	0.18 (1.06)	53.25 (3.12)	0.64 (p<0.01)
Northern islands (n=28)								
Ordinary least squares	2.98 (1.01)	15.39 (3.57)	-15.51 (-1.14)	-120 (-0.34)	88.68 (1.52)	-0.44 (-1.67)	78.28 (4.02)	0.56 (p<0.01)
Spatially lagged	0.62 (0.23)	16.09 (4.16)	-11.77 (-1.03)	-107 (-0.36)	82.85 (1.70)	-0.42 (-1.94)	83.45 (5.90)	0.66 (p<0.02)
Spatial error	3.18 (1.22)	15.72 (4.15)	-15.88 (-1.35)	-117.54 (-0.38)	88.76 (1.76)	-0.44 (1.00)	85.26 (4.81)	0.65 (p<0.02)
Southern islands (n=17)								
Ordinary least squares	-11.44 (-1.02)	-8.77 (-0.6)	4.35 (0.2)	143776 (4.41)	-60.21 (-1.40)	0.1 (0.46)	89.18 (3.22)	0.84 (p<0.09)
Spatially lagged	-12.93 (-1.60)	-9.59 (1.04)	3.03 (0.20)	130004 (5.30)	-50.42 (-1.71)	0.14 (1.00)	87.35 (4.60)	0.94 (p<0.01)
Spatial error	-2.31 (-0.55)	1.81 (0.40)	-13.51 (-1.60)	14859 (9.75)	-21.87 (-1.19)	0.26 (2.65)	89.21 (4.92)	0.97 (p<0.01)

Of the independent variables employed, there was a notable consistency in relative contribution to explaining the observed variation in the number of plant species recorded. For the models applied to all islands, distance to mainland was the strongest predictor of the number of plant species, while in the northern sector, longitude was consistently the strongest predictor and in the southern sector, island area was consistently the strongest predictor.

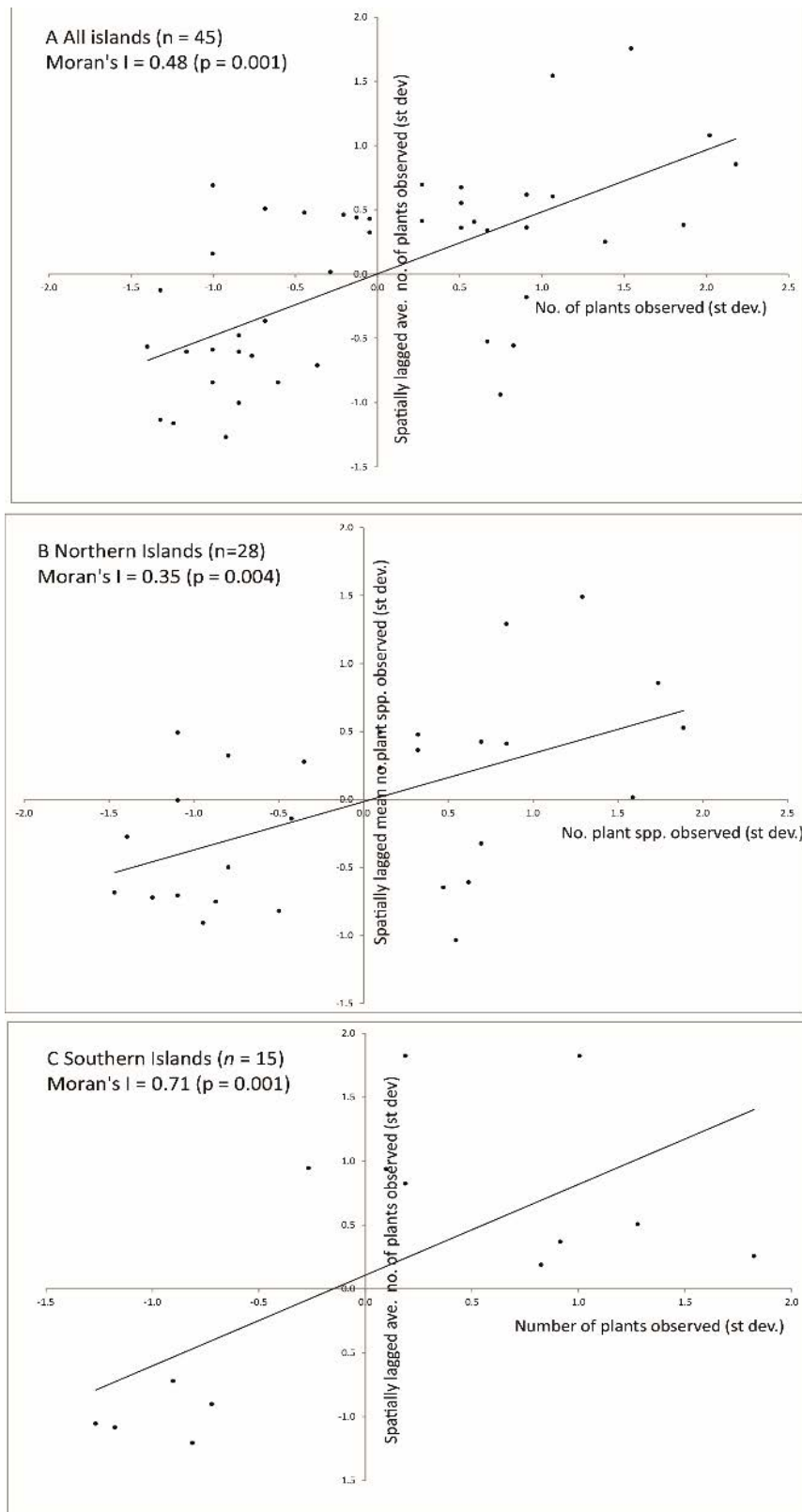


Figure 2. Univariate Moran scatter plot of spatial autocorrelation for A. All 43 islands along the Great Barrier Reef, B. Northern islands, and C. Southern islands.

DISCUSSION AND CONCLUSIONS

The higher levels of autocorrelation observed in the southern islands relative to the northern islands, alongside the consistent better performance of the regression models here, may relate to the historical development of the islands. More plant species are supported by the islands in the north than those in the south (an average of 22 species per island in the northern sector, as opposed to 15 in the southern sector). This is driven in part by a much greater degree of endemism in the northern islands, with 330 species known only north of Cairns (16°45'S), compared to 33 known only to the Capricorn-Bunker Islands (Stoddart and Fosberg, 1991). Such a remarkable disparity means that the greater range of species in the north affords a greater opportunity for variation in plant species number supported by the northern islands, thereby reducing their potential for autocorrelation. One notable environmental difference between the northern and southern islands is the depth of the surrounding GBR lagoon floor, which is much deeper in the southern (ranging from -29 to -70 m) than the northern sector (-7 to -28 m). The varying sea level histories, both along and across the continental shelf, mean that the position of an island will determine the time-range over which it has accumulated (Hopley et al., 2007). All of the sampled reef islands reached sea level and infilled their lagoons and reef flats over the Holocene, although those in the south likely experienced a temporal lag corresponding to the additional time taken to reach sea level from a deeper antecedent lagoon shelf.

Radiocarbon dating of interior island sediments has suggested that deposition at the southernmost island (Lady Elliot) began around 3200 years ago (Chivas et al., 1986) whilst sediments from the northern cay (Bewick) indicate island building there began earlier, 5000–4000 yr BP (Kench et al., 2012). There are also several notable islands in the northern sector (e.g., Two Isles, Three Isles, East Hope) that have high terraces reaching around 5 m above current sea level (McLean et al., 1978; Stoddart et al., 1978). It is therefore possible that older islands in the north may be less autocorrelated because they have had a longer time to reach a dynamic equilibrium with their local environments. Stoddart and Fosberg (1991) distinguish between older, higher sand cays in the approximate age range of 2900–3400 yr BP that support closed canopy woodland and younger, lower terraces of average age 2700 years that support low shrubs, herbs, vines and grasses.

There also remains the possibility that flora of the larger forested islands is relict from the last glacial period (ca. 8000 years BP), when the modern reefs were superimposed on the dry northern coastal shelf (Stoddart and Fosberg, 1991). Thus, the statistically discernible spatial patterns of the plant communities might express variable sea level history and associated island age along the latitudinal extent of the GBR (McLean et al., 1978). To further perpetuate this distinction, Buckley (1981) notes the likelihood of a slower response rate to environmental changes of the northern 'forest-tree' islands relative to the southern 'strandline' islands. Despite the widespread supply of propagules by fruit eating birds or human visits across all the islands studied, these may give rise to variable timescales over which metapopulation dynamics and dynamic equilibria may emerge between mean plant species richness and local environmental conditions.

Unique features of islands that lend themselves well to the statistical analysis of populations include their relatively isolated geographical setting and ease with which boundary conditions can be specified (Whittaker and Fernández-Palacios, 2007). Islands also have minimal resident human populations and few impacts from economic development and resource extraction, making them particularly attractive case studies (Sanmartín et al., 2010). Several regional (i.e., island-group) scale studies have sought to explain the distribution of plant diversity in relation to potential causal factors in the British Isles (Johnson and Simberloff, 1974), the Galápagos islands (Connor and Simberloff, 1978), Nui Atoll in the Pacific (Woodroffe, 1986), Hawaiian Islands (Price, 2004) and British Columbia (Cody, 2006). These studies have considered how geographical place and associated local environmental context influences islands and the plants they support. Such considerations empirically investigate the relationship between regional biophysical conditions and plant communities. Characterisation of this relationship is attractive because it allows prediction of longer-term island vegetation community response to future anticipated conditions. Such predictions are useful for environmental management decision-making and extend the traditional scope of biogeographical work from mapping distributions and

explaining associated patterns to the development of theoretical and deterministic propositions about how the vegetation of low lying islands responds to environmental conditions (Graves and Reavey, 1996). As part of this approach, spatial models offer a unique opportunity to incorporate terms that reflect interaction between sites, accounting for geographical space. In this case, the marked and consistent growth in explanatory power of the spatial models that incorporated island neighbourhoods implied that these interactions have an important role. These have not been explicitly incorporated in previous statistical investigations of plant species numbers across the sand cays of the Great Barrier Reef.

In the context of island biogeography, neighbourhood effects are largely driven by modes of dispersal. For example, *Pisonia grandis* fruits become attached to birds such as the Black Noddy and Bridled Tern through a sticky resinous residue and are subsequently transported over water (Chen and Krol, 2004). The Indo-Pacific character of the southern island plant communities indicates dispersal across the GBR from this region. Drift disseminules of 34 plant species that were collected on the cays of the Swains Reefs suggest inward flow from the New Caledonia-Vanuatu-Fiji region, facilitated by the East Australia current (Smith et al., 1990). Similar studies have noted the viability of drift seeds and fruit on Raine Island in the northern GBR originating from either northern Australia or Papua New Guinea (Hacker, 1990).

Because of the paucity of herbaceous plant species in the fossil record, support for the longer-term continental influence on woody plant species composition in the northern sector has been through phytogeographic observations. For example, the common woodland tree species in the north (including *Aglaia elaeagnoidea*, *Diospyros maritima*, *Eugenia carrisoides*, *Exocarpos latifolia*, *Ficus opposita*, *Manilkara kauki*, *Mimusops elengi*, *Pouteria obovata*, *Terminalia arenicola*, and *Terminalia muelleri*) align much more closely to those associated with northern continental Queensland than the southern islands, whereas both *Pisonia* and *Pandanus*, which occur on the southern sand cays, are uncommon in the north (Stoddart and Fosberg, 1991). The rate of extinction of existing species is likely to be heavily influenced by episodic disturbance events, such as storms, cyclones and associated mechanical damage driving large scale species turnover (Flood and Heatwole, 1986), but also through chronic disturbances such as saltwater intrusion into the freshwater lens upon which many plant species are fundamentally reliant (White and Falkland, 2010). Neighbourhood influences in immigration and extinctions may also arise through spatially-structured environmental processes, such as regional variation in rainfall. Mean annual rainfall in the northern islands, such as Green Island (2152 mm) and Low Isles (2027 mm) is substantially greater than that recorded for Heron Island further south (965 mm), such variability might be due to a combination of the mountainous Queensland coastline, southeast trade winds and the inter-tropical convergence zone.

Neighbourhood effects were stronger among the islands of the southern sector, where regressions of island plant species against variables depicting the geographical context also consistently performed better relative to those applied to both the northern islands and the entire GBR datasets. For the southern sector, island area emerged as the strongest predictor of plant species number, in accordance with conventional island biogeography theory and earlier findings on the primary importance of island area (Heatwole, 1991; Whitehead and Jones, 1969). Island area might be important because of the enhanced probability that larger islands will be reached by dispersing propagules (Buckley and Knedlhans, 1986), or the greater habitat diversity and associated range of ecological niches on larger islands, resulting in reduced competition for resource utilisation (Tilman et al., 1997). Variation in edaphic factors, including surface phosphatisation, the relative proportion of sand and shingle; the presence or absence of ground-nesting sea-birds and human interference are also likely related to island size. Substrate gradients from beach to interior are also particularly marked on larger reef islands and likely translate to a greater range of vegetative expression (Heatwole, 1991).

The spatial models presented here may be improved by the use of anisotropic methods that account for the associated directional dependence of marine environmental processes, such as ocean currents that may drive the dispersal of plant seed propagules and the ability of islands to intercept these (Buckley and Knedlhans, 1986). It may also be useful to control for the fact that many of the cays of the Great Barrier Reef have been significantly modified by human activities, including the removal of guano and rock phosphate, military bombing and shelling, plantation of coconut palms, the introduction of goats

and exotic plant species (e.g. *Lantana spp.* and prickly pear, *Opuntia spp.*) and the development of infrastructure such as tourist resorts and airstrips (Daley, 2014). From an ecological perspective, it may be instructive to include the diversity of common plant associations (Table 1) in the regression model as an indicator of functional groupings, particularly those occurring in different stages of island vegetative succession (Heatwole, 2011), alongside the potential for competition to occur. Nevertheless, in a world increasingly worried about the effects of human activity, such spatially-explicit empirical linkages between plant numbers on reef islands and their biogeographical surroundings allow predictions as to how future plant communities might change for a range of environmental circumstances.

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