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Depth and latitudinal gradients of diversity in seamount benthic communities

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Abstract

Aim: Latitudinal and bathymetric species diversity gradients in the deep sea have been identified, but studies have rarely considered these gradients across hard substratum habitats, such as seamount and oceanic island margins. This study aimed to identify whether the current understanding of latitudinal and bathymetric gradients in α -diversity (species richness) apply to seamount ecosystems, as well as ascertaining whether identifiable trends were present in seamount β -diversity along a bathymetric gradient.

Location: Exclusive Economic Zones of Saint Helena, Ascension Island and Tristan da Cunha, spanning 8–40°S in the South Atlantic.

Taxon: Seamount megabenthic communities.

Methods: Images from 39 transects, collected between 250 and 950 m, were used to characterise species richness. We subsequently applied general linear models to test possible environmental drivers across latitudinal and bathymetric ranges. Regression models were employed to investigate the β -diversity gradient of species turnover with depth.

Results: Transects in temperate latitude had significantly higher species richness than those in the tropics. Surface primary productivity and substrate hardness both had significant positive effects on species richness, and a weak relationship between temperature and species richness was observed. No significant relationship between species richness and depth was detected, but there was significant species turnover with depth.

Main conclusions: Seamounts and oceanic islands do not conform to established depth–diversity relationships within the depth range studied. However, seamounts and oceanic islands in the South Atlantic do appear to follow a parabolic latitudinal diversity gradient, closely associated with higher productivity in temperate regions.

KEYWORDS

deep-sea ecology, diversity gradient, South Atlantic, spatial ecology

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1 | INTRODUCTION

Latitudinal diversity gradients (LDGs) are one of the most well-researched natural patterns in the world but the driving mechanisms remain unclear (Gaston & Spicer, 2004; Pianka, 1966; Rohde, 1992). In terrestrial systems, most taxa including trees, mammals, and reptiles display a parabolic relationship whereby species richness is greatest in the tropics, and decreases poleward (Begon et al., 2006). Similarly, in coastal marine ecosystems, LDGs are often parabolic for taxa such as molluscs and fish (Clarke & Crame, 1997; Rohde, 1992; Roy et al., 1998), although not all taxa adhere to this relationship (Kendall & Aschan, 1993).

The deep sea represents a third system where LDGs have been considered, but at present, there is no consensus on the patterns and drivers. Some studies show a poleward decline in diversity/richness comparable with terrestrial and shallow water ecosystems (Culver & Buzas, 2000; Hillebrand, 2004; Rex et al., 1993, 2000), some show a poleward increase (Lamshead et al., 2000; Tietjen, 1984), and some show a unimodal relationship per hemisphere with highest diversity/richness falling within temperate latitudes (Rosa et al., 2008; Woolley et al., 2016). Explanation of these trends considers both evolutionary scale processes and present ecological conditions. The former refers to patterns driven by environmental parameters over geological time-scales. For example, the Norwegian Basin has a depressed modern-day diversity in multiple taxa (Culver & Buzas, 2000; Rex et al., 1993). Explanations for this include insufficient time for replenishment since Quaternary glaciation; and major sediment inflows 6000–8000 years ago causing local extinctions (Rex et al., 1997). Historical ecology is often merged with biogeography to explain inter-regional differences in diversity and richness. For example, the South Atlantic is hypothesised as being more species rich than the North Atlantic (Culver & Buzas, 2000; Gage, 2004) due to its continuity with other oceans (the Indian and Pacific), as well as being less impacted by glaciation during the Quaternary Period (Wilson, 1998).

Modern ecological explanations of LDGs refer to how the environmental parameters of the present attempt to explain observed patterns. The most notable environmental parameter mentioned in almost all deep-sea LDG studies is productivity, for example, particulate organic carbon (POC) flux to depth (Bodil et al., 2011; Corliss et al., 2009; Culver & Buzas, 2000; Gage, 2004; Lamshead et al., 2000, 2002; McClain et al., 2012; Rex et al., 1993, 2000; Rosa et al., 2008; Smith et al., 2008; Tittensor et al., 2011; Yasuhara et al., 2009). Net primary production in surface waters is driven by photosynthesis of phytoplankton. Organic matter, in the form of decaying phytoplankton and faecal pellets, sinks through the water column and, although large amounts are remineralised by bacteria, a small proportion (ca. 0.5%–2%) reaches abyssal depths (Smith et al., 2008). The POC flux that reaches the seafloor acts as the main or only food source for many deep-sea ecosystems and often showing peaks in temperate latitudes (Lutz et al., 2007). Diversity driven by food supply is consistent with the species-energy hypothesis (Hutchinson, 1959), which suggests the amount of available energy sets limits to the richness of the system.

Within the deep sea, bathymetric diversity gradients (BDGs) have attracted significant research (Danovaro et al., 2008; Howell et al., 2002; Levin et al., 2001; Olabarria, 2005, 2006; Rex et al., 2005). The deep sea, here defined as occurring below 200 m, is not uniform due to considerable variability in abiotic characteristics, such as pressure and temperature with depth. This change in the physical environment with depth is reflected in observed changes in diversity, with peak diversity in many taxa between 200 and 4000 m attributed to comparatively higher energy availability (than deeper waters) and greater environmental stability (than shallower waters) generating more ecological and evolutionary opportunities (Brandt et al., 2004; Gage et al., 2000; Rex, 1973; Rex et al., 2006). However, similar to investigations into LDGs, results can be mixed, with a number of studies not recognising any BDG (Bodil et al., 2011), or a multimodal one. Allen and Sanders (1996) and later Olabarria (2005) both reported that bivalve diversity increased with depth in the northeast Atlantic. Contrary to this, other studies have identified decreasing diversity with depth in foraminiferans (Lagoe, 1976) and isopods (Svavarsson et al., 1990). In gastropods positive, negative and unimodal relationships between diversity and depth have been observed across 10 basins (Stuart & Rex, 2009).

Much less is known about deep-sea β -diversity, the variation in species diversity between two habitats or regions comprising one or a combination of species loss/gain (nestedness); or species replacement (turnover). Along bathymetric gradients, β -diversity trends have largely been interpreted as attributable to turnover (Carney, 2005; McClain & Hardy, 2010; Victorero et al., 2018). An example of where nestedness may dominate the β -diversity trend is in regions where diversity is depressed due to food scarcity, for example, in the abyss (Wagstaff et al., 2014). Rex et al. (2005) showed that abyssal macrofaunal molluscs were actually nested subsets of lower bathyal communities (abyssal populations had densities too low to be reproductively viable, and therefore act purely as a sink for bathyal populations). In regions where food supply is not limited in the abyss, turnover dominates, reflected in the presence of abyssal endemics (Brault et al., 2013).

Most deep-sea studies looking at both latitudinal and BDGs have focused on sampling infaunal communities in soft-sediment areas such as abyssal plains or continental slopes using equipment not suitable for collecting data on hard substrates (Culver & Buzas, 2000; Lamshead et al., 2002; Rex et al., 1993, 2000). Multi-taxon studies of both diversity gradients from hard-bottom or more complex habitat types, such as seamounts, are rare (McClain & Lundsten, 2015; McClain et al., 2010; Victorero et al., 2018).

Seamounts are commonly defined as large topographic features that rise at least 1000 m above the surrounding seafloor and occur throughout the world's oceans (Rogers, 1994). They are associated with higher levels of production due to the entrapment of zooplankton over the summit during diurnal migration, and upwelling of nutrient-rich, deeper water facilitating primary production (Clark et al., 2010). Effects of increased primary production cascade up the trophic chain with seamounts often being active foraging grounds for pelagic taxa, sometimes referred to as 'hotspots' when surrounded by comparatively

oligotrophic ocean (Hosegood et al., 2019). Some seamounts break the surface forming oceanic islands that support similar biological communities to seamounts (Mazzei et al., 2021). Although not fully understood, the hydrodynamic regimes encircling both seamounts and oceanic islands are thought to be complex and energetic (Bell et al., 2021; Chivers et al., 2013; Levin & Thomas, 1989; Roden, 1991; Turnewitsch et al., 2013; Vlasenko et al., 2018), with enhanced currents associated with increased food supply and exposed hard substrate. Seamounts are topographically complex, with varying substrate types, including rocky walls and ledges, and biogenic reef communities comprising sponges and corals (Auster et al., 2005; Clark et al., 2010; Davies et al., 2015; Rogers, 1994), contrasting with soft-sediment habitats that often surround their base. Although not heavily documented, changes in assemblage structure along bathymetric gradients on individual seamounts have been described (Davies et al., 2015; McClain et al., 2010; Morgan et al., 2019). McClain et al. (2010) did not observe a gradient in α -diversity with depth on a northeast Pacific seamount. However, they found substantial assemblage structure changes with depth, suggesting that high β -diversity can ultimately be responsible for the increased total biodiversity of seamounts. However, due to the small number of studies focusing on the diversity patterns on seamounts, it is difficult to substantiate broad generalisations of their diversity–depth relationship (Clark et al., 2010; Davies et al., 2015; McClain et al., 2010).

The aims of this paper are to investigate changes in seamount diversity across depth and latitude, specifically to answer two questions. First, does the current understanding of latitudinal and bathymetric gradients in α -diversity apply to South Atlantic seamount ecosystems? The limited sampling of seamounts, combined with the fact they provide hard substrate in an otherwise relatively soft substrate dominated deep ocean, means these features may subvert our current understanding of diversity gradients. Knowledge on whether seamount ecosystems conform to the current understanding of diversity gradients will facilitate more targeted protection in the future, as well as contribute to our understanding of regional and global deep-sea diversity patterns. The second question this paper aims to answer is: are identifiable trends present in seamount β -diversity (turnover) along a bathymetric gradient? The limited literature focused on change in community structure along environmental gradients on seamounts does suggest bathymetric β -diversity trends may be observed (Bridges et al., 2021; McClain et al., 2010; Morgan et al., 2019; Victorero et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Study area

Saint Helena, Ascension and Tristan da Cunha (henceforth referred to as St Helena, Ascension and Tristan) are governed as a single UK Overseas Territory (UKOT) in the South Atlantic Ocean (Figures 1 and 2). These oceanic islands have steep sides, descending into deep water close to shore. Ascension forms part of the mid-Atlantic Ridge,

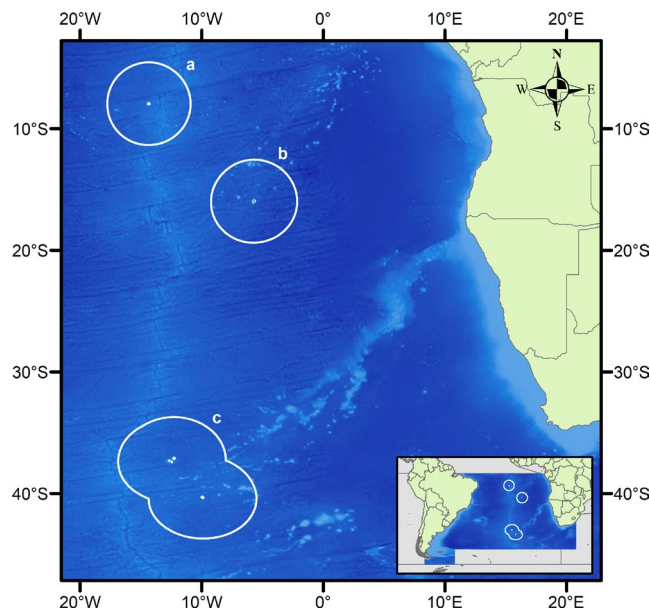


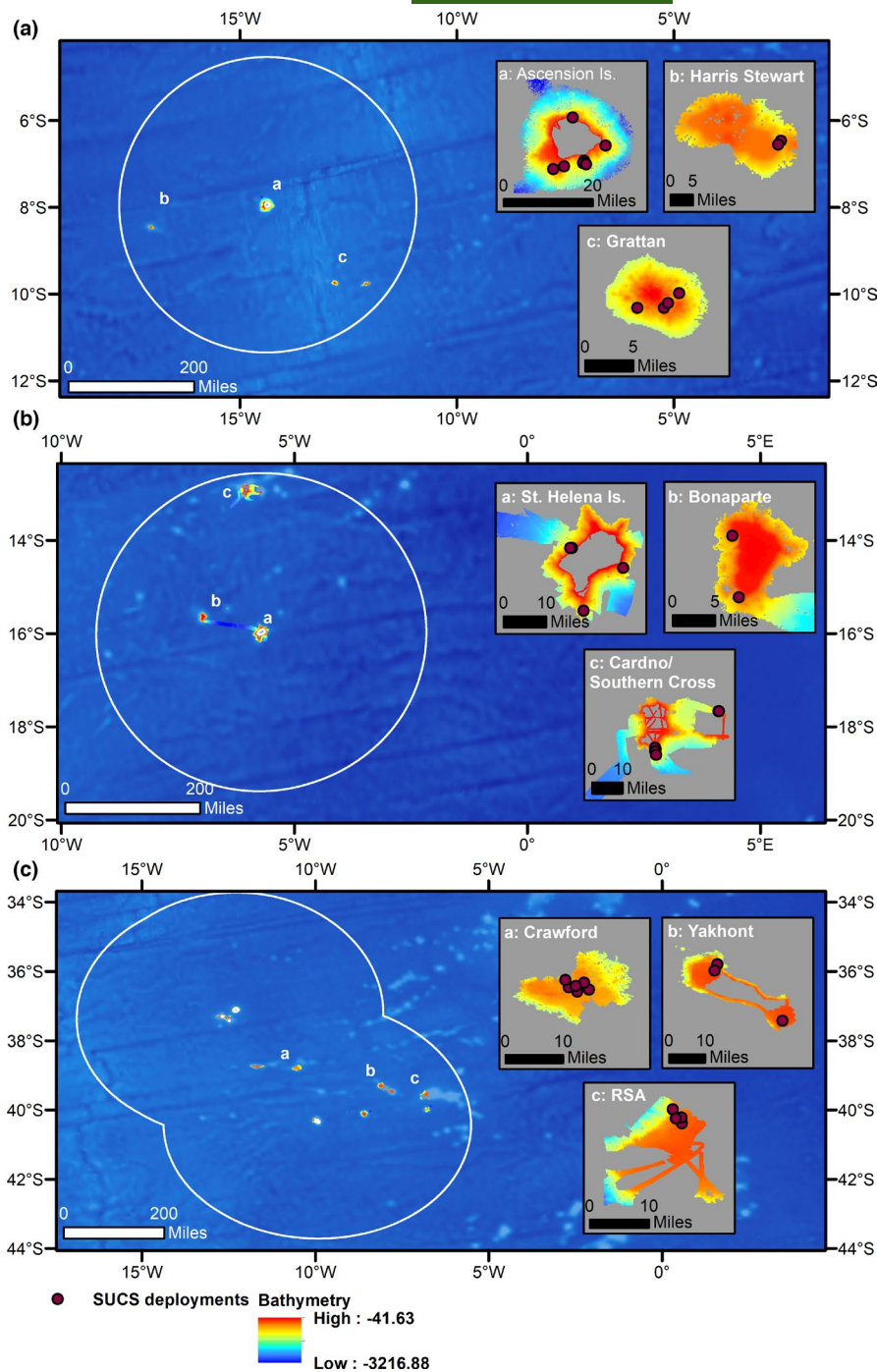
FIGURE 1 The Southeast Atlantic Ocean. The exclusive economic zones of Ascension Island (a), Saint Helena (b) and Tristan da Cunha (c) are drawn in white and correspond to Figure 2a–c. Underlying bathymetry is from the General Bathymetric Chart of the Oceans (GEBCO_2014 Grid, version 20150318). Map drawn in WGS84

St Helena forms part of the Guinea seamount chain, and both are located within the tropics, whereas Tristan is temperate and found at the most south westerly point of the Walvis Ridge. Over 90% of each of their exclusive economic zones (EEZs) are comprised of waters deeper than 1000 m.

2.2 | Sampling methods

A bespoke camera lander (Shallow Underwater Camera System [SUCS], Supporting Information S1) was used to collect image data in cluster transects ($n = 39$) across nine different seamounts and oceanic islands. Cluster transects refer to groups of images, haphazardly spaced between 5 and 10 m of each other, with all images from an individual transect taken within 100 m of each other to capture relevant environmental heterogeneity. The minimum number of images in one transect was 16; subsequently random number generation was used to remove additional images in all transects to control for bias in the area sampled. The SUCS tripod design settles perpendicular to the seafloor and capture high-resolution images of 0.14 m² area using a 5-megapixel Allied Vision Prosilica GC2450 camera, a Fujinon HF12.5SA-1 lens and twin variable intensity lights, all controlled from a desktop computer on ship. While the SUCS is appropriate for the collection of imagery to characterise benthic assemblages, some areas of extremely high slope cannot be sampled. An Ultra Short Base Line (USBL) beacon mounted on the camera lander allowed for an accurate Global Positioning System (GPS) position to be obtained.

FIGURE 2 (a–c) Shallow Underwater Camera Systems (SUCS) deployments plotted on high-resolution (25 m) multibeam bathymetry across: (a) three sites within the Ascension Island exclusive economic zone (EEZ); (b) three sites within the St Helena EEZ, and (c) three sites within the Tristan da Cunha EEZ. Underlying bathymetry from General Bathymetric Chart of the Oceans (GEBCO_2014 Grid, version 20150318). Map drawn in WGS84



All data were collected during the 2015 (Barnes et al., 2015), 2017 (Barnes et al., 2019) and 2018 (Morley et al., 2018) cruises of the RRS *James Clark Ross*, and a 2019 cruise on the RRS *Discovery* (Whomersley et al., 2019). There are 13 transects from each UKOT EEZ (henceforth referred to as territories), within which three seamounts/islands (henceforth referred to as sites) were sampled per territory. A breakdown of the sampling structure is presented in Table 1 with transect depths available in Supporting Information.

Multibeam seabed mapping using Kongsberg EM122 and EM710 multibeam echosounders allowed for characterisation of sites prior to equipment deployments to ensure suitability for the SUCS. Temperature, salinity and other environmental profiles were

recorded using a CTD (conductivity, temperature and depth) sensor at each transect.

2.3 | Image analysis

Six hundred and twenty-four images were quantitatively analysed using IMAGEJ (Schneider et al., 2012) or subsequently BIIGLE 2.0 (Langenkämper et al., 2017) which facilitated comparable annotations but was found to be more efficient and fit for purpose. All organisms identified as distinct morphotaxa were assigned an operational taxonomic unit (OTU). OTUs were identified to the highest

Territory	Site	No. of images per site	No. images per territory
Ascension Island	Ascension Island	112	208
	Grattan seamount	64	
	Harris-Stewart seamount	32	
Saint Helena	Bonaparte seamount	32	208
	Cardno/Southern Cross seamount complex	96	
	Saint Helena island	80	
Tristan da Cunha	Crawford seamount	96	208
	Yakhont seamount	48	
	RSA seamount	64	

TABLE 1 Sampling structure indicating the number of images per territory and per site

taxonomic resolution possible. All individuals were counted, with encrusting and reef-forming species recorded as percentage cover. For these OTUs, values used were either 1% (as most were only present in very small abundances), or between 10% and 100% in 10% increments. The benthic assemblage composition is described in Bridges et al. (2021) and blue carbon ecosystem services in Barnes et al. (2021).

Primary and secondary substrate types were recorded using the following categories based on Wentworth (1922): bedrock, reef framework, live reef, cobbles, coral rubble, pebbles, coral gravel, gravel and sand (Supporting Information S1). Images were assigned a substrate hardness score based on the types and proportions of each substrate observed on a 6-point scale where 1 would equate to 100% sand and 6% to 100% bedrock. For example, if 50% of the image comprised sand and 50% comprised rock, the hardness score would be 3 to weight each appropriately.

2.4 | Environmental data preparation

Multibeam files were gridded at 25 m cell size in QPS QIMERA and projected into Goode Homolosine Ocean (an equal-area projection) in ArcGIS v10.7. The Benthic Terrain Modeller plugin (Walbridge et al., 2018) was used to derive rugosity, slope, broad- and fine-scale bathymetry position index (BBPI and FBPI respectively) and curvature from the bathymetry. Inner and outer radii for BBPI and FBPI were 8 and 40 and 1 and 8, respectively, facilitating identification of megahabitats >1 km (e.g. banks and plateaus) and mesohabitats 200 m–1 km (e.g. gulleys and reefs sensu Greene et al., 1999). Using the 'mgcv' package (Wood, 2011) in R (R Core Team, 2019) a generalised additive model (GAM) was used to create a bottom temperature layer for each territory from CTD casts undertaken during the same cruises, together with archived data in the British Oceanographic Data Centre database, containing data supplied by Natural Environment Research Council. Details of the GAMs for each territory are supplied in Supporting Information S1. Depth, latitude and longitude were tested individually and in all possible combinations as predictors of temperature. Temperature records were partitioned for each territory at an 80/20 training/test split, and the

test dataset used to validate modelled predictions. For all three territories, depth was selected as the only predictor of temperature; in all cases, Pearson's correlation coefficient between the in-situ test observations and predictions was 0.99 (2 d.p.), suggesting predictions were strongly in line with recorded temperatures.

Particulate organic carbon flux to depth values at 5 arcmin resolution (approximately 9.2 km at the equator) derived from (Lutz et al., 2007) were resampled and re-projected to 25 m resolution in Goode Homolosine Ocean. Mean surface primary productivity data were downloaded from Bio-Oracle (Assis et al., 2018), and also resampled and re-projected from 5 arcmin to 25 m. Resampling does not alter the resolution of the underlying data, it only splits cells into a gradient of smaller cells to allow for raster stacking when mapping.

2.5 | Statistical analysis

2.5.1 | α -diversity gradients

To confirm whether depth and substrate had been sampled evenly across territories, parametric statistics were employed using the 'car' package (Fox & Weisberg, 2019) in R. Both variables were normally distributed and homogenous in variance, and therefore a one-way analysis of variance (ANOVA) was calculated for each variable to determine if there were significant differences in transect depths and substrate hardness between territories. A Pearson's correlation test was used to determine if there was a significant relationship between depth and substrate hardness. There was no significant difference in the substrate hardness ($F_{[2, 36]} = 2.52, p > 0.05$) nor depths sampled ($F_{Tu} = 0.84, p > 0.05$) within each territory and no correlation ($-0.16, p > 0.05$) between depth and substrate hardness (Supporting Information S2). This confirmed that the data from each territory were comparable, allowing for investigations into the effects of depth and latitude on diversity. A one-way ANOVA and a Tukey's honest significant difference (HSD) post-hoc test were run on species richness to assess significant differences between territories and identify the strength of differences respectively.

To explore possible drivers of α -diversity trends, a general linear mixed model was constructed in R, specifying territory as a random

effect. The random effect explained no variance and therefore, following model redundancy, general linear models were used (representing the most parsimonious approach). Prior to building, all variables were investigated for correlation. Correlates with coefficients $\geq \pm 0.7$ were subject to further testing with GAMs, resulting in only one correlate being used (Supporting Information S2). Hereafter, surface primary productivity is considered a proxy for latitude. Primary productivity is more ecologically and biologically relevant than latitude, and also allows for better contextualisation within the wider literature.

Two general linear models were initially built, one using depth and one using temperature, alongside the following variables: surface primary productivity, temperature, POC flux to depth, substrate hardness, BBPI, FBPI, slope, curvature and rugosity. These models were permuted across 10 randomly subsetted sets of 16 images per transect to ensure any detectable trends were stable. To further explore results and as the relationship between temperature and depth is known to vary with latitude, models for each territory were also constructed.

2.5.2 | β -diversity gradients

β -diversity across the bathymetric range was investigated using mantel tests and beta regression models from the 'betareg' package (Cribari-Neto & Zeileis, 2010) in R. The data were subset to create separate datasets for each territory. Using the 'vegan' package (Oksanen et al., 2019), pairwise Jaccard dissimilarity (d_{ij}) matrices (on abundance data) and Euclidean distance dissimilarity matrices (i.e. absolute difference in depth) were constructed for each territory. Species turnover along the depth gradient was measured by plotting pairwise Jaccard similarity ($s_{ij} = 1 - d_{ij}$) against pairwise absolute difference in depth. For each of these, a distance-decay model was fitted to the points using a beta regression model. Although beta regression models are intended for use when the response variable, y , is $0 < y < 1$, when using the betareg package, a minor transformation is required. This was following Smithson and Verkuilen (2006):

$$\tilde{y} = \frac{y \times (n - 1) + 0.5}{n},$$

where n = sample size. One pairwise comparison at St Helena was removed as the two transects that were spaced close together and so were not considered to be independent. Although exponential models are often employed to describe distance decay (Millar et al., 2011), we found that beta regression models were more appropriate due to the small sample sizes within this dataset. The y -axis intercept ($\times 100$) of each model is interpretable as the expected percentage similarity between two transects at the same depth. Mantel tests were carried out on the Jaccard dissimilarity and Euclidean distance dissimilarity matrices to further characterise the relationship between depth and biological dissimilarity. The y -axis intercepts, slope values and mantel correlations were then compared across the territories as per Anderson et al. (2013).

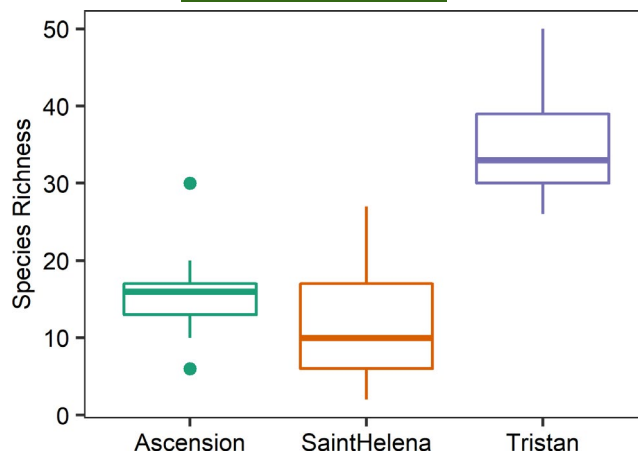


FIGURE 3 Mean species richness for each South Atlantic UK Overseas Territory. An ANOVA revealed significant differences ($p < 0.01$) between Tristan and the other two territories. Dots above and below the boxplot for Ascension indicate outlier transects

3 | RESULTS

3.1 | α -diversity gradients

Mean species richness was significantly different between territories (ANOVA: $F_{[2, 36]} = 37.23$, $p < 0.01$; Figure 3). There were significant differences between Tristan and Ascension, and Tristan and St Helena (Tukey's HSD, both $p < 0.01$) but Ascension and St Helena had similar species richness (Tukey's HSD, $p > 0.05$).

An initial general linear model identified surface primary productivity (a proxy for latitude), substrate hardness and temperature as significant predictors of species richness, all having positive effects and explaining approximately 72% of the variation in species richness (Table 2).

However, when permuted 10 times by randomly subsetting a different set of 16 images per transect, the weakly significant relationship between temperature and species richness did not hold (mean average p -value of 0.065 across an additional 10 models, Supporting Information S2). Depth and temperature were strongly correlated, and therefore to ascertain whether depth was also a significant driver, a second model was constructed substituting temperature for depth and permuted. Depth was not identified as significant using the original subset, nor any of the further 10 permutations (Supporting Information S2). General linear models for each territory individually revealed that temperature was only a significant predictor of species richness at St Helena (Supporting Information S2).

3.2 | β -diversity gradients

Fitted beta regression models for all three territories are detailed in Table 3 and plotted in Supporting Information. All three models identified absolute difference in depth as a significant predictor of

TABLE 2 Metrics for the initial general linear model run on species richness of seamounts in the South Atlantic. Bold font is used to denote significant predictors

	Estimate	SE	t value	p-value
Intercept	-14.776	7.429	-1.989	0.056
Surface primary productivity	4.288 × 10³	6.063 × 10²	7.073	<0.001
Substrate hardness	3.459	1.027	3.368	<0.01
Temperature	1.670	0.808	2.066	0.048
Particulate organic carbon flux to depth	-0.330	0.311	-1.058	0.299
Rugosity	1.677	2.207	0.760	0.454
Slope	0.180	0.119	1.480	0.149
Broad-scale bathymetry position index	-0.022	0.023	-0.951	0.349
Fine-scale bathymetry position index	0.017	0.168	0.104	0.918
Curvature	0.486	1.271	0.380	0.705

TABLE 3 Results from the beta regression model fits of beta diversity as turnover along a depth gradient in three South Atlantic UK Overseas Territories, and for the mantel correlations for each

Territory	Slope (turnover with depth) ± SE	y-axis intercept (3 d.p.)	Mantel Rho (3 d.p.)
Ascension	$1.85 \times 10^{-3} \pm 6.9 \times 10^{-4}$	0.053	0.390
St Helena	$1.35 \times 10^{-3} \pm 6.3 \times 10^{-4}$	0.034	0.318
Tristan	$3.08 \times 10^{-3} \pm 6.05 \times 10^{-4}$	0.152	0.539

similarity, concurring with the significant correlations identified by the Mantel tests (Table 3).

The degree of turnover in benthic communities with depth is measured by the slope of the models (Table 3). The slope of the Tristan model is significantly steeper than those for Ascension and St Helena, suggesting the rate of turnover is higher in temperate latitudes than tropical. Tristan also has the highest modelled similarity between transects at the same depth (15.2%), with equivalents for Ascension (5.3%) and St Helena (3.4%) being much lower (Table 3), demonstrating that there was more within-depth-stratum variation in communities in the tropics. Correlations between the biological and depth dissimilarity matrices were all significant ($p < 0.05$) but varied in strength with Tristan being highest and Ascension and St Helena being similar (Table 3).

4 | DISCUSSION

Our observations suggest that productivity represents a key driver in species richness between ecosystems on temperate and tropical South Atlantic seamounts, and that while depth-related gradients are apparent in β -diversity, there is no bathymetric α -diversity gradient present across the depth range studied.

Increased surface primary productivity is the most likely driver of the higher species richness found at Tristan, echoing links between productivity and richness described in other studies investigating LDGs across different deep-sea habitats (e.g. Culver & Buzas, 2000;

Lambshhead et al., 2000; Rex et al., 2000; Tittensor et al., 2011). The notable difference in our results is the significant relationship between species richness and surface primary productivity, but not POC flux to depth. Tittensor et al. (2011) and McClain et al. (2012) argue the importance of energy in explaining deep-sea LDGs. Energy in the deep sea can be broadly categorised into two types: thermal and chemical. Thermal energy (i.e. temperature) can drive LDGs in the deep sea, particularly over geological time-scales of ~100,000 years (Hunt et al., 2005). Chemical energy is largely composed of POC inputs from overlying waters. Increasing depth leads to decreasing POC flux as organic matter is remineralised and sinks through the water column (Lutz et al., 2007). This study focussed upon upper bathyal depths (<1000 m; Supporting Information S2) and therefore is likely to be more influenced by surface productivity than in deeper waters (e.g. >2000 m) where bacterial remineralisation has had the chance to act, representing a disconnect between the surface and seafloor. This may therefore provide a reason as to why surface primary productivity strongly influences species richness, but POC flux to depth does not. Rosa et al. (2008) investigated the drivers of diversity in pelagic cephalopods in the Atlantic Ocean, finding higher diversities at temperate latitudes. Following Rutherford et al. (1999), these diversity patterns were attributed to differences in upper-ocean thermal structure allowing for weaker stratification in temperate latitudes. The more gradual temperature change in a thermocline with a deep base, as seen in temperate latitudes, may facilitate more niches per unit area than a sharp thermocline with a shallow base, as often seen in tropical latitudes, resulting in higher diversity. The surrounding pelagic environment is critical in shaping benthic substrate, so seamount benthic communities and diversity patterns are likely affected by stratification regimes in the upper ocean, particularly on features with shallow summits. Consequently, differing stratification regimes may explain why we observe higher species richness in temperate latitudes than tropical.

If the species richness of seamounts and oceanic islands in the South Atlantic is driven by surface primary productivity, then the lack of significant difference in species richness between Ascension and St Helena is perhaps unsurprising as both territories are characterised by similarly low levels of surface primary productivity



(Supporting Information S2). Additionally, if productivity is the key driver of α -diversity, any underlying LDG is unlikely to be of uniform steepness from the equator, poleward. This is because the majority of the South Atlantic Ocean represents reasonably oligotrophic water, while temperate latitudes facilitate comparatively higher productivity due to the active frontal zones (Lutz et al., 2007; Peterson & Stramma, 1991). This theory could lend some explanation as to why differences in α -diversity are identifiable over large latitudinal ranges (e.g. perhaps $>10^\circ$), but not smaller ranges closer to the equator. Variable strength relationships between latitude and diversity were also described by Gage (2004) for the Atlantic, but the existence of an LDG in the South Atlantic has previously been questioned. Rex et al. (1993) identified 'significant inter-regional variation' in the South Atlantic, but not a directional LDG, assigning a portion of the observed variation to patterns in the strength and variability of surface production. Similarly, Gage (2004) studied the large-scale biodiversity patterns of Cumacea (Peracarida: Crustacea), finding that when South Atlantic samples were separated out, linear regression relationships between diversity and latitude were not significant. However, authors did highlight that sparse data from the South Atlantic would likely limit the ability to detect significant relationships if they were to exist. Of course, aspects of historical ecology could be at play when considering the differences in species richness between territories. While all three territories are part of larger ridge systems or seamount chains, at the depths sampled in this study, Ascension and Saint Helena are more isolated than Tristan. According to MacArthur and Wilson's (1967) theory of island biogeography, increased isolation leads to decreased biodiversity due to limited immigration possibilities and thus our results align with this.

The finding that α -diversity is significantly higher on features at Tristan than tropical sites is likely a result of Tristan's close proximity to the subtropical front (STF), where subtropical and subpolar waters converge (Smythe-Wright et al., 1998). Frontal zones increase surface primary productivity (Franks, 1992) and consequently support a diverse range of pelagic taxa (Bost et al., 2009), perhaps explaining why species richness at Tristan is comparatively high. Not only does the enhanced productivity equate to increased energy supply which would lead to higher species richness (Hutchinson, 1959), further ecological concepts such as resource partitioning, where multiple taxa use different parts of a resource, could be further driving species richness by reducing interspecific competition (Schoener, 1974).

The lack of an identifiable BDG agrees with the results of McClain et al. (2010) who also found no consistent bathymetric pattern in α -diversity on a seamount in the Northeast Pacific. Authors suggest a number of theories why this might be, including: (1) the seamount's proximity to productive coastal waters masking any bathymetric productivity gradient that would drive species richness; and (2) the sampling of largely hard substrate. Although the former is not applicable to this dataset due to the isolated nature of all three territories, the sampling of hard substrate could be shaping our results, particularly because the sampling restrictions of the SUCS under-represent steeper areas and cliffs, and thus potentially

misses additional biodiversity. However, the range of substrate hardness sampled at each territory was not significantly different, and therefore although this represents a bias, it would in theory be uniform across all transects. Unimodal BDGs are typically recorded in soft sediment areas where the communities largely comprise macrofaunal, deposit-feeding taxa (Rex et al., 1997). For these types of organisms and communities, POC flux (that decreases with depth) may represent the only food delivery mechanism and therefore would be very important in regulating species richness. In contrast, Lundsten et al. (2009) reported that hard substrate seamount communities tend to be dominated by suspension feeders that remove food from the surrounding water, utilising currents to maximise yield. Seamounts are hydrodynamically complex, so it is plausible that if taxa rely on currents as their food delivery mechanism, rather than passively sinking detritus, traditional bathymetric α -diversity gradients may not be observed. Another reason that there is no observed BDG could be a result of the size classification of taxa. Only megafaunal taxa were recorded in this study, and Rex (1981) reports that megafaunal taxa display weaker unimodal relationships with depth than macrofaunal taxa that are typically characterised by infaunal communities, with some exceptions (Howell et al., 2002). This said, the lack of relationship between depth and species richness is somewhat surprising when you consider the presence of a (weak but sometimes significant) relationship between temperature and species richness, and the strong correlation between depth and temperature ($0.94, p < 0.001$). This significant relationship may be driven by a slightly larger temperature range ($+0.7^\circ\text{C}$) being sampled at St Helena, hence the significance of temperature in the individual territory model (Supporting Information S2). However, it is well established that the relationship between temperature and depth varies with latitude and it is therefore possible that the weak significance reflects this. This said, the identification of temperature as a significant predictor of species richness in one model does align with the species-energy hypothesis, and other studies. For example, O'Hara and Tittensor (2010) identified temperature as the *only* significant predictor of species richness of ophiuroids across 60 seamounts, based on data from 100 to 3000 m, but similarly found no evidence of a unimodal peak in diversity with depth. Even so, due to the disappearance of the significant relationship upon permutation of the data, further research is required to confirm whether temperature is a significant driver of α -diversity on seamounts at this broad spatial scale. Similarly, the lack of an observed BDG may be due to the narrow depth range sampled, nevertheless, one would perhaps expect to see some increase in species richness from 200 to 1000 m if a unimodal relationship between depth and species richness with a peak in bathyal depths was present.

Although there is no change in α -diversity with depth, the β -diversity analysis highlights significant bathymetric β -diversity gradients in the form of turnover (i.e. species replacement). These findings are similar to those of McClain et al. (2010) who also observed significant changes in β -diversity with depth, but a lack of a relationship between α -diversity and depth. McClain and Rex (2015) provide a review of β -diversity in the deep-sea benthos and surmise

that latitudinal β -diversity gradients are more moderate than bathymetric β -diversity gradients, likely because the rates of environmental change are greater across depth than they are latitude. We cannot statistically test turnover along a latitudinal gradient because the small size of the dataset does not allow for division into enough distinct depth bands; we can however discuss bathymetric β -diversity gradients in the context of latitude. The significantly higher slope value of the beta regression model for Tristan suggests the rate of species turnover with depth may change with location in the South Atlantic. Additionally, the relationship between dissimilarity and depth is considerably stronger for Tristan (Table 3). Both these results may be observed because of the stronger stratification of water mass structure at Tristan due to proximity to the STF as water mass structure is a known driver of community structure (Bett, 2001; Howell et al., 2002; Koslow, 1993; Tyler & Zibrowius, 1992). Productivity hotspots are known to influence bathymetric species turnover, whereby increased productivity drives faster turnover as seen at Tristan (McClain & Rex, 2015). Therefore, proximity to the STF may not only be shaping α -diversity gradients, but β -diversity too by facilitating the creation of more niches thanks to variable water mass structure and productivity regimes.

The lower expected similarities between transects at the same depth in the tropics (and therefore higher β -diversity) is perhaps counterintuitive when considering the significantly lower α -diversity compared to temperate latitudes (Figure 3). Bridges et al. (2021) characterised the communities at all three territories using this dataset and additional data, finding that tropical assemblages were characterised by low evenness and were heavily dominated by fewer species than the temperate communities. This would explain the high within-depth-stratum variation but low α -diversity in tropical regions, because the number of species are fewer, but the number of significantly different communities are high.

Much of the literature focused on β -diversity gradients on seamounts identifies turnover as the major component (Carney, 2005; McClain & Hardy, 2010; McClain et al., 2010; Victorero et al., 2018), and thus investigation of nestedness, the second component, was deemed out of scope for this manuscript. This said, it is therefore important to acknowledge that our findings must be caveated with the point that there may be further underlying trends in β -diversity attributable to nestedness that are not observed within our results.

5 | CONCLUSION

Although there is comparatively little hard substrate habitat in the deep sea, seamounts and oceanic islands remain important ecosystems for the provision of food, connectivity and refugia (Rogers, 1994, 2018). Species richness, a measure of α -diversity, of seamount ecosystems in the South Atlantic appears largely driven by surface primary productivity and is thus higher in temperate latitudes than the tropics. Although no polar transects were available,

the comparatively lower surface primary productivity compared to temperate regions (Assis et al., 2018) would suggest that seamounts and oceanic islands in the South Atlantic perhaps follow a parabolic LDG. There was no relationship between depth and α -diversity within the depth range sampled, although significant bathymetric β -diversity gradients were observed. There is a high level of variability in both the observed diversity patterns on seamounts and the environmental parameters that are deemed important in shaping said patterns across different seamount focused studies (McClain et al., 2010; Morgan et al., 2019; O'Hara & Tittensor, 2010; Victorero et al., 2018). Inconsistency in the ability to identify environmental parameters important for *all* seamount benthic communities again demonstrates the heterogeneity in seamount habitats. Our observations suggest that current understanding of LDGs in deep-sea species richness does apply to seamount ecosystems in the South Atlantic, but as suggested in Clark et al. (2012), in order to be able to make any generic statements about seamount ecology, particularly at the global scale, environmental and biological characterisation of more seamounts is required, particularly those in data-poor areas and across different productivity regimes. The difference between the relationships of α - and β -diversity with depth in this study demonstrates that both types of diversity should be considered when characterising seamounts.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.b5mkkwhbw>.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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