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A closer examination of the 'abundant centre' hypothesis for reef fishes

Hagar Yancovitch Shalom[1,2] | **Itai Granot**[1] | **Shane A. Blowes**[1,3] | **Alan Friedlander**[4] | **Camille Mellin**[5,6] | **Carlos Eduardo Leite Ferreira**[7] | **Jesús Ernesto Arias-González**[8] | **Michel Kulbicki**[9] | **Sergio R. Floeter**[10] | **Pascale Chabanet**[11] | **Valeriano Parravicini**[12] | **Jonathan Belmaker**[1,2]

[1]School of Zoology, Tel Aviv University, Tel Aviv, Israel

[2]The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

[3]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[4]Department of Biology, University of Hawaii, Honolulu, HI, USA

[5]Australian Institute of Marine Science, Townsville, Queensland, Australia

[6]The Environment Institute and School of Biological Sciences, University of Adelaide, Adelaide, South Australia, Australia

[7]Departamento de Biologia Marinha, Universidade Federal Fluminense (UFF), Niterói, Brazil

[8]Laboratorio de Ecología de Ecosistemas de Arrecifes Coralinos, Centro de Investigación y de Estudios Avanzados del I.P.N, Unidad Mérida, Mérida, Yucatán, México

[9]IRD (Institut de Recherche pour le Développement), Laboratoire d'Excellence Labex Corail, UMR IRD-UR-CNRS ENTROPIE, Université de Perpignan, Perpignan, France

[10]Marine Macroecology and Biogeography Lab, Depto. de Ecologia e Zoologia, CCB, Universidade Federal de Santa Catarina, Florianopolis, Santa Catarina, Brazil

[11]UMR ENTROPIE, IRD, Université de La Réunion, CNRS, Labex CORAIL, La Réunion, France

[12]EPHE, PSL, USR 3278 CRIOBE, Perpignan, France

Correspondence
Jonathan Belmaker, School of Zoology, Tel Aviv University, Tel Aviv, Israel.
Email: jonathan.belmaker@gmail.com

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Abstract

Aim: The 'abundant centre' hypothesis states that species are more abundant at the centre of their range. However, several recent large-scale studies have failed to find evidence for such a pattern. Here we used extensive global data of reef fishes to test the 'abundant centre' pattern, and to examine variation in the abundance patterns across species using life history and ecological traits.

Location: Marine habitat at a global extent: from Indo-Pacific to Atlantic reefs.

Methods: We used underwater visual estimates of fish abundance, containing 22,963 transects and 1,215 species. For each species we calculated the slope between abundance and distance to the range centre, with the range centre estimated using four different methods. We tested whether abundance patterns differ between the range core and margins using segmented regression. Meta-analytic methods were used to synthesize results across species, and to test whether species traits can explain variation in the fit to the pattern among species.

Results: The method used to define the range centre had a large effect on the results. Nevertheless, in all cases we found large variation between species. Results of the segmented regression revealed that changes in abundance across the range core are very small and that steep declines in abundance happen only towards the range margins. Body size and mean abundance were the main traits affecting the fit to the pattern across species.

Main conclusions: We find large variation across species in the fit to the abundance centre pattern. Nevertheless, we do find support for a general pattern of a range core with high, but variable, abundance and steep decline in abundance towards the range periphery. Thus, species do tend to be rare at the range margins, making them sensitive to extirpation due to both natural and anthropogenic impacts.

KEYWORDS

'abundant centre hypothesis', abundance, meta-analysis, occupancy, reef fish, segmented regression

1 | INTRODUCTION

Understanding variation in abundance, both within and across species, is a central ecological question (Brown, Mehlman, & Stevens, 1995; Gaston, 1994; Jones, Caley, & Munday, 2002; Preston, 1948; Pulliam, 1988). A commonly evoked hypothesis postulates that populations farther from their geographical range centre will be less abundant, a pattern known as the 'abundant centre' hypothesis (Brown, 1984; Sagarin & Gaines, 2002b). This hypothesis has implications for a wide range of other ecological and evolutionary patterns and processes such as population dynamics and gene flow (Sagarin, Gaines, & Gaylord, 2006).

While the 'abundant centre' pattern has been originally considered ubiquitous (Brown, 1984; Brown et al., 1995; Husak & Linder, 2004; Sorte & Homfman, 2004), empirical tests of this pattern have found mixed results (Pironon, Papuga, Angert, María, & Thompson, 2017; Sagarin & Gaines, 2002b). Specific analyses vary greatly in their fit to an 'abundant centre' pattern, with some species displaying a good fit and others contradicting it (e.g. species with the highest abundance in one of the range edges) or simply showing no consistent pattern at all (Husak & Linder, 2004; Sagarin & Gaines, 2002a; Samis & Eckert, 2007). In marine systems, little support was found for the 'abundant centre' pattern in two intertidal mollusc species (Tam & Scrosati, 2011), two barnacles (Wares & Castaneda, 2005) and porcelain crabs (Rivadeneira et al., 2010) but stronger support for a different barnacle species (Scrosati & Freeman, 2019) and a limpet (Fenberg & Rivadeneira, 2011). For fishes, few studies have examined the 'abundant centre' pattern, usually finding little supportive evidence (Liedke et al., 2016; Tuya, Wernberg, & Thomsen, 2008).

Difficulties in finding generalities in abundance patterns across species ranges may stem from the heterogeneity of the methods used to estimate abundance. However, two recent large-scale analyses have examined a large number of species using standardized sampling and still found limited evidence for the 'abundant centre' pattern (Dallas, Decker, & Hastings, 2017; Santini, Pironon, Maiorano, & Thuiller, 2019). Thus, to date there seems to be weak support for consistent variation in abundance across species ranges. Nevertheless, a recent global study on reef fishes found strong support for a peak in abundance at the thermal centre of the species range (Waldock, Stuart-Smith, Edgar, Bird, & Bates, 2019). This means that either: (a) reef fish are exceptional in conforming to the 'abundant centre' pattern, or that (b) methodological differences between Waldock et al. (2019) and previous studies (such as Dallas et al., 2017; Santini et al., 2019) have created difference in the ability to detect 'abundant centre' patterns.

While the original version of the hypothesis refers to the centre of a geographical range (Brown, 1984), others have tested environmental range centres (e.g. using the species climatic niche to set the range centre, Dallas et al., 2017; Santini et al., 2019; Waldock et al., 2019). Some studies have found that environmental range centres conform better to the 'abundant centre' pattern than geographical range centres (Martínez-Meyer, Díaz-Porras, Peterson, & Yáñez-Arenas, 2013). However, processes such as Allee effects, heterogeneous spatial structure and non-equilibrium dynamics can lead to low correlation between environment and abundance (Osorio-olvera, Soberón, & Falconi, 2019). In addition, species may decline in abundance away from a location of peak abundance which is neither at the geographical nor environmental range centre. This could be due, for example to biotic interactions dictating the location of peak abundance to be outside the environmental range centre. Finally, differences between core and marginal populations may be minimal, regardless of the methods used to define the range centre (Dallas et al., 2017; Pironon, Villellas, Morris, Doak, & García, 2015; Santini et al., 2019). In reef fishes, declines in abundances were found away from a thermal optimum (Waldock et al., 2019) but it is unclear whether this also corresponds to declines in abundance away from the geographical centre of the range.

The 'abundant centre' pattern has most often been tested using a monotonic association between abundance and distance from range centre (Figure 1b). However, it is possible that abundance steeply

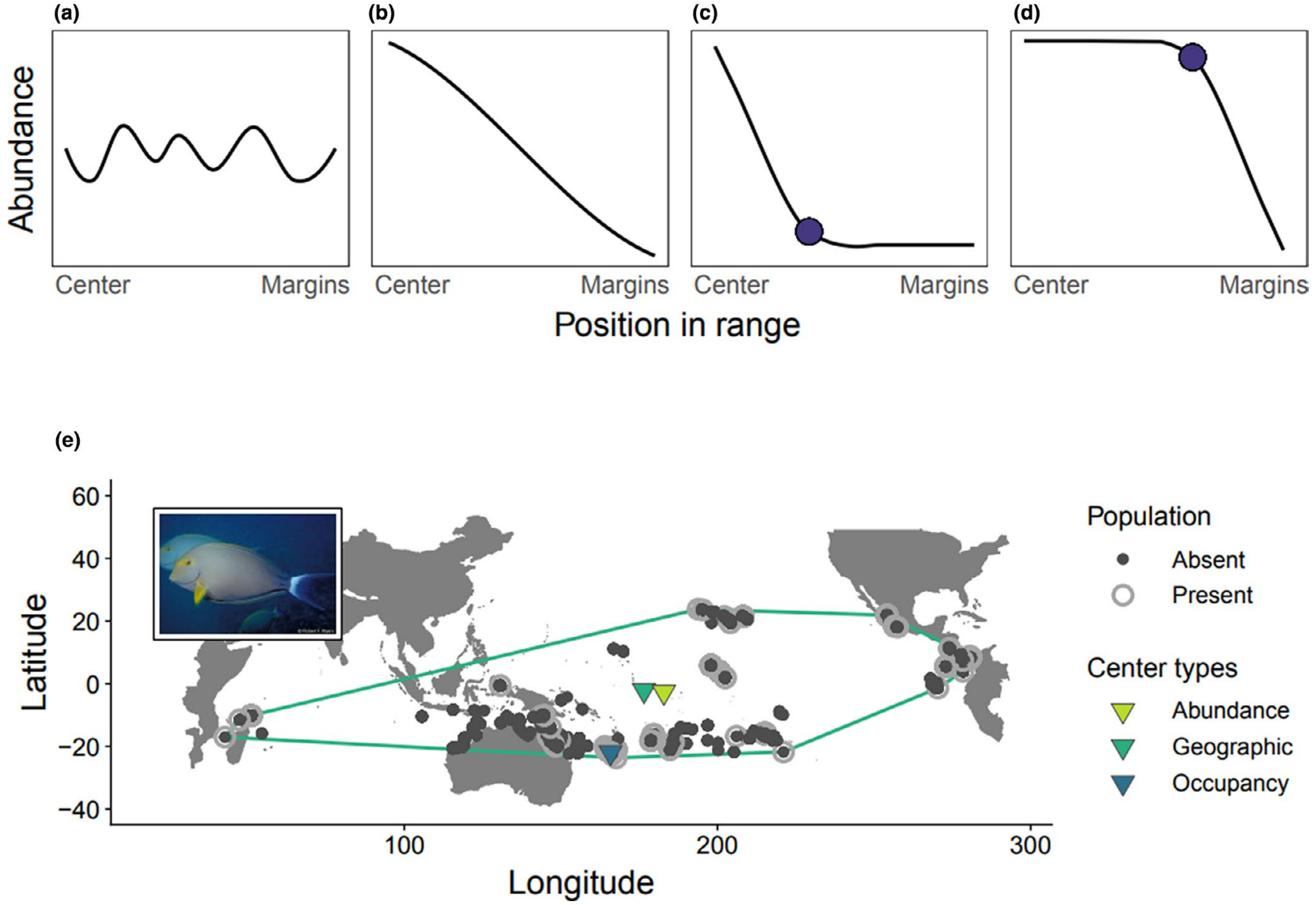

FIGURE 1 (a-d) four different hypothetical shapes of the 'abundant centre' pattern: (a) no relationship between abundance and the position within the range; (b) decline in abundance is monotonic; (c) steep decline in abundance mostly at the range centre, abundance remains consistently low at the margins; (d) decline in abundance occurs mostly towards the range margins. Points represent breaking points were abundance changes abruptly. (e) Example of a species range (*Acanthurus xanthopterus*) with the position of the different centres and the range area set by the convex hull of the sites where the species was found. Photo credit Robert F. Myers. The maps use geographical latitude / longitude projection

declines near the range centre followed by a region of low abundances (Figure 1c) (Mcgill & Collins, 2003) or that abundance is high over the range core and only declines towards the range margins (Figure 1d). Studies such as Dallas et al. (2017) and Santini et al. (2019) use correlation coefficients for the analyses. While these methods can detect both linear and nonlinear relationships, they do not allow to differentiate between the scenarios presented in Figure 1. For example both Figure 1c and d may display equal correlation coefficients although the underlying pattern is very different. Other studies used nonlinear methods, such as generalized additive quantile regressions, to detect 'abundant centre' patterns (Waldock et al., 2019). However, the range of patterns produced by additive models may make generalizations difficult. Here, we were explicitly interested in testing for potential breaks in the abundance-distance relationship, where a species may display one pattern in the range centre and a different pattern in the range periphery (Figure 1). Hence, we explicitly test for non-monotonic variation in abundance across the range, using segmented regressions, to better understand the structuring processes.

Finally, very few studies have examined how patterns of abundance across the range change among species (but see Dallas et al., 2017; Santini et al., 2019). In other words, how different traits affect the variation in abundance patterns. For example large species are generally less abundant than small species (White, Ernest, Kerkhoff, & Enquist, 2007). Species with low abundance, for purely statistical reasons, are likely to show weaker gradients in abundance across their range, so we may expect less abundant species to provide weaker support for the 'abundant centre' pattern. As another hypothesis, we may expect large bodies species to be long-lived, suggesting potentially more stable population dynamics. This would lead to situations where populations may be small but survival is high enough to partially offset the role of demographic stochasticity and lead to clear 'abundant centre' pattern. Thus, examining the 'abundant centre' pattern across a multitude of species traits can reveal the ecological and statistical mechanisms underlying variation in abundance across large spatial scales.

In this study, we used a large and standardized dataset of 1,215 species of coral reef fishes with a global extent from Indo-Pacific to Atlantic coral reefs, and examined how abundance varies across species ranges. Specifically, we contrasted four different methods for estimating the range centre, and examine whether abundance changes monotonically or abruptly with distance from these centres. Finally, we examined whether these patterns vary predictably across species that differ in their traits. The results aimed to reconcile previous studies that found little evidence of an 'abundant centre' pattern (Dallas et al., 2017; Santini et al., 2019) with a recent study on reef fishes that found strong evidence for such a pattern (Waldock et al., 2019), and thus take a fresh view at understanding spatial patterns of abundance.

2 | MATERIALS AND METHODS

2.1 | Species data

We compiled a comprehensive dataset of reef (both coral reefs and rocky reefs) fish abundances based on underwater visual surveys collected by trained SCUBA divers. We used two large existing datasets (Figure 2a); the Reef Life Survey (RLS) dataset containing 2,367 fish taxa from 2,773 sites (Edgar & Stuart-Smith, 2014) and the GASPAR group dataset that documents 1,809 fish taxa from 375 sites (Kulbicki et al., 2011). The surveys were made along belt transects located in different depths (1–50 m) on hard substrate. All individual fish observed along the search area were identified and number of individuals (i.e. abundance) recorded as the divers swam slowly along the transect.

The belt-transect methodology offers an easy convert abundance to density units (unlike other methodologies, such as stationary point-counts or using trapping data). Transect dimensions differed, with most transects being either 500 m^2 (50 m × 10 m), 100 m^2 (25 m × 4 m) or 40 m^2 (20 m × 2 m). Thus, we standardized each species density across all transects sizes to 100 m^2. Abundance estimates from visual surveys are sensitive to sampling biases, and some of the species might be under estimated (e.g. cryptic and small). However, since this bias is likely to be similar across the species range, this should not impact our results. We excluded species observed along fewer than 10 transects; species that are not reef

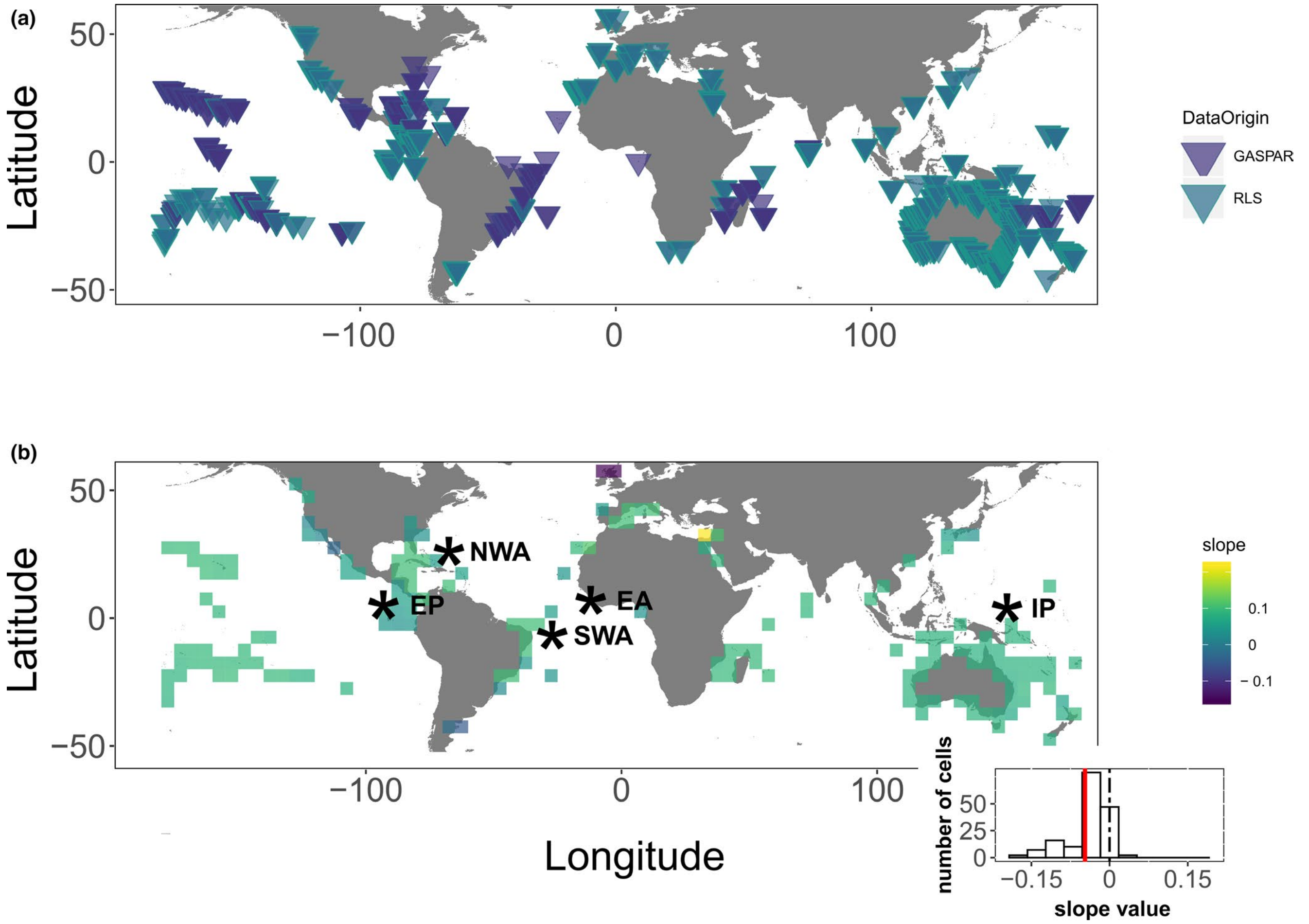

FIGURE 2 (a) The location of the surveyed transects. Each colour represents a different data source the GASPAR group (purple) and the reef life survey (RLS, blue). (b) The average cell-wise slope of the relationship between abundance and distance to the *Occupancy centre*. The stars represent mid domains (following Parravicini et al., 2013). The insert shows the distribution of the cell slopes, dashed line is located at zero and red line is located at the mean slope across all cells. IP—Indo-Pacific, EP—East Pacific, NWA—NorthWest Atlantic, SWA—SouthWest Atlantic, EA—East Atlantic. The maps use geographical latitude / longitude projection

associated; and circumtropical species for which it is difficult to define a range centre. After data cleaning, 22,963 transects and 1,215 species remained for analysis.

2.2 | Estimating change in abundance across ranges

Each species range was set as the convex hull polygon around all the sites where it was present ('*chull*' function in the R package '*grDevices*') (Figure 1e) to define the extent of occurrence (following Gaston, 1994; Gaston & Fuller, 2009). While we agree using IUCN range map estimates could have been desirable, this is unfortunately not possible. At a species level, only 564 species out of the 1,215 presented in our data have IUCN range maps assessments to date. At a family level the situation is even worse with only 14 families (from the 87 present in our data) assessed, indicating severe taxonomic bias. Hence, we based our range estimates on the actual surveys.

Reef habitat itself is inherently patchy and the persistence of reef fish is not possible over much of the estimated range of the species, for example within the large expanses of open ocean. However, as transects were confined to reef habitat we focus on habitat patches that are potentially suited for reef fish, and can then ask if abundance on these patches confirms to the 'abundant centre' hypothesis. While the patchiness does not preclude estimating patterns of local abundance across the range, it may impact processes such as dispersal among patches and meta-population dynamics. These may either reinforce or weaken 'abundant centre' patterns, but are not explicitly examined within this study.

To determine how the abundance of each species changes from the range centre to the range margins, we compared several alternative methods to define the location of the range centre, and an alternative method examining the distance of each location to the closest range margin.

2.2.1 | Geographical centre

The geographical centre of the range, estimated as the centroid of the range ('*centroid*' function – '*geosphere*' package).

2.2.2 | Abundance centre

We also identified the location where species abundance is the highest. We used this centre to assess the validity of the 'abundant centre' hypothesis, even if the peak in abundance does not correspond to the geographical range centre. For example, species may be most abundant within a particular environmental condition at the edge of the range and decline predictably from that peak. In this case, when examining the *Geographical centre* alone we may conclude that abundance increase towards the range margins. We are well aware of the circularity of using the abundance centre to test the abundant centre hypothesis. However, this method was used for two main reasons. First, it provides us with a clear upper limit for the slope of decay in abundance across space. If the slope of this relationship is much higher than the slope found for other centres (geographical centre, occupancy centre or distance to range margins, see below) it may mean that a clear pattern of a peak in abundance within the range is indeed present, but not detectable when using the other methods to define the range centre. Second, if this method fails to provide a clear slope, it means that a pronounced peak in abundance within the range is simply not present (e.g. Figure 1a).

We identified the abundance centre as the centroid of the top decile of sites at which the species was most abundant in terms of the number of individuals. This was done in order to reduce the importance of a single site which may have anomalously high abundance. However, results were similar when we used the single most abundant site as the abundance centre.

2.2.3 | Occupancy centre

Several studies have tested the 'abundant centre' hypothesis using environmental space instead of geographical space (Dallas et al., 2017; Martínez-Meyer et al., 2013; Pironon et al., 2015; Santini et al., 2019; Waldock et al., 2019). However, here the ability to detect an 'abundant centre' pattern may be strongly affected by the methodology. Raw output of species presence-background niche modelling algorithms (such as MaxEnt) do not estimate environmental suitability but the similarity between the environments where the species was found to the environments in the background, which may explain the weak correlations between environmental suitability and species density (Osorio-olvera et al., 2019). In this study, we prefer to side-step these methodological issues and examine the 'abundant centre' hypothesis in geographical space, while using the regions of highest occupancy as a proxy for the highest environmental suitability.

Thus, we defined an *Occupancy* range centre as the location where a species occupancy (proportion of sites in which the species is present) is the highest. To estimate the *Occupancy centre*, species ranges were first extended to a rectangle with an addition of 1° on each side, then divided into 2° × 2° cells, and occupancy was calculated by dividing the number of transects where the species was present by the total number of transects in the cell. The occupancy centre was calculated as the centroid of the top decile of cells with the highest occupancy. In all subsequent analyses, we did not use transects in which the species was absent. Thus while absences are used to define the *Occupancy centre*, we do not expect a statistical correlation between abundance and occupancy as they are estimated using different data. That is not to say that other factors may not produce a correlation between abundance and occupancy (we elaborate on this in the discussion).

2.2.4 | Distance to range margin

Species may have little variation in abundance within the range centre, but decrease towards the range margin as the physical or biological environment changes more rapidly (Figure 1d). To evaluate this hypothesis, we calculated the shortest distance of each point inside the range to the closest point that lies along the range margin ('dist2Line' function, '*geosphere*' package).

To standardize for variation in absolute abundance among species, we calculated for each species relative density as the proportion of individuals at a site relative to the maximal number of individuals of that species. Then, for each different method, the relative density of individuals ($\log_{10}$ transformed) was regressed against the distance in km ('distGeo' function, '*geosphere*' package) from the range centre or the margin ($\log_{10}$ transformed). We note that we do not know if changes in abundances across the range depend more on absolute distance or relative distances. Hence, we also tested an index of relative position within the range (Enquist, Jordan, & Brown, 1995; Fenberg & Rivadeneira, 2011). This was computed as the distance of each site to the range centre divided by the sum of the distance to the range centre and the distance to the closest range margin. Thus, this index varies between zero (site on range centre) and one (site on range margin). The results are present in Figure S1. However, as the general patterns do not change depending on the method used we retain only the results using absolute distance in the main text.

Abundance may be influenced by local habitat attributes as well as by variation in sampling design among studies. We thus used depth, and data source as covariates within each model. To account for potential species-specific impacts of habitat loss and fishing on abundance patterns we used location within marine-protected areas (MPAs) as an additional covariate (site in or out of MPA). This allowed us to control for anthropogenic impact on abundance across global scales and for many species without obtaining species-specific habitat requirement estimates.

Within each species range there were many transects where the species was not found (i.e. zero abundance) that were used to calculate the *Occupancy centre*. There are good reasons to both exclude and include these locations with abundances of zero in such analyses. On the one hand, including zeros may conflate occupancy patterns with patterns in abundance. Species may be absent from locations within the range because of many processes, such as those related to habitat availability. We may want to separate those from processes that determine abundance once the minimal conditions for the species to be present within the location are met. Thus, transects with no individuals may represent samples at which the depth or other local habitat requirements were sub-optimal, but may not be representative of large-scale abundance gradients. On the other hand, if the processes that determine abundance and presence are similar, it also makes sense to use the information contained within the locations with zero abundances. However, in practice, when we run the analyses including or excluding locations with zero abundances we obtained very similar results (see Figure S2). Hence, in the reminder on the manuscript we only show the results excluding zeros.

We used Gaussian OLS regressions, especially as after the exclusion of zeros these models represented a good fit to the data. To further account for the potential of zero inflation to bias model fit, we also used negative binomial models and quantile regressions. The results confirm that these alternative methods did not: (a) change the relative support for the different centres; (b) change the relative explanatory power of species traits, or (c) improved the explanatory power of the models. We present the results of the quantile regressions in the appendix (Figure S3), but retain the Gaussian OLS results in the main text.

We used a meta-analytic approach to synthesize patterns across the 1,215 species using the regression slope as the effect size (response variable; 'rma' function, '*metafor*' package). We here follow Koricheva, Gurevitch, and Mengersen (2013) and define meta-analysis as statistical methods for combining the magnitudes of the outcomes (effect sizes) across different datasets, in our case species (see also Santini et al., 2019). This was done for all four types of range centres, and for both the linear and segmented regressions. In all these analyses, we used the species-specific partial slope as the effect size, weighted by the slope's inverse-variance (one over its estimated variance). Hence, species for which we had better confidence in the slope (e.g. for which we had more records and hence lower variances) received higher weighting. For the segmented regressions we summarized both slope estimates and the breaking point.

2.3 | Segmented regression

Changes in abundance across the range need not be linear. Some studies (Dallas et al., 2017; Santini et al., 2019), use correlation coefficients to detect changes in abundance across the range. While this sidesteps the issue of linear verses nonlinear relationships, it still assumes the relationship to be monotonic (always increasing or always decreasing). Another solution, is to explicitly model the potential nonlinearity (e.g. using generalized additive models, Waldock et al., 2019). However, the range of patterns detected may make generalizations difficult. Here, we were explicitly interested in testing for potential breaks in the abundance-distance relationship, where a species may display one (linear) pattern in the range centre and a different (linear) pattern in the range periphery (Figure 1).

To determine whether abundance patterns across the range are monotonic or display abrupt changes, we used segmented (piecewise) regressions ('segmented' function, '*segmented*' package). The segmented regression seeks two distinct lines with different slopes. The breaking point is set such that the sum of the residuals for both slopes is minimized. To assist the interpretation of this analysis, we left distances untransformed (i.e. measured in km). We used Davies test to check if the two slopes are significantly different one from each other ('davies.test' function, '*segmented*' package).

2.4 | Grid-based analyses

Geography and history may play major roles in shaping abundance patterns (Parravicini et al., 2013; Renema et al., 2008). To examine geographical variation in the distance-abundance patterns, we divided the world into 5° × 5° cells. Each cell was considered to belong to one out of five oceanic domains separated by major geographical barriers following Parravicini et al., (2013). For each cell, we calculated the weighted average of the slope estimates from the abundance-distance regressions for all the species in the cell, using the multiplicative inverse of the standard error of the slope as weights (thus, slopes were essentially weighted by the variation in the estimate of the slope itself). Therefore, species with less data and that contained more variable slope estimates are down-weighted. Then, we assessed how the weighted-averaged slope per grid cell changes across several grid-scale variables that are hypothesized to impact the steepness of the abundance-distance relationship. These include: (a) Distance from the domain centre. Distance from domain centre is used here as a proxy for isolation, with more isolated grids expected to have steeper abundance-distance relationships. (b) Absolute latitude. Higher latitudes have steeper environmental gradients which may cause steeper abundance-distance relationships. (c) Reef area. Larger reef areas can impact occurrence probability and abundances via meta-population dynamics (Hanski, 1998). We used reef area within a grid cell and area of shallow water habitat <50 m as additional predictors. As coral reef area is only relevant to coral reef we confined this predictor to grid cell between latitudes of −37.5° and 32°.

Analyses were performed globally for all domains together, adding domain as a predictor, and then separate analyses were made for each domain. We accounted for spatial autocorrelation, using simultaneous autoregressive (SAR) models (Dormann et al., 2007). We examined a range of possible neighbourhood sizes (500–3,000 km), and chose 1,000 km as it was with the lowest Akaike information criterion (AIC) score ('spautolm' function, '*spdep*' package).

2.5 | The effect of traits on abundance patterns across species

We collected information on ecological and life-history traits for all species and examined whether they explained variation in the slopes. These traits included mean abundance, range size, body size, diet, fishing sensitivity, distance to the Coral Triangle and latitude. For a full explanation of the predicted impact of these traits and how these were derived see Appendix A. Correlations between variables can be seen in Figure S4, but were generally low ($r < 0.28$), except for a high correlation between the size of the fish and sensitivity to fishing ($r = 0.81$). For the trait analyses, we removed species that did not have all the seven traits or those having extreme values (absolute values of the regression slope higher than one, mean abundance values higher than 500 individuals in transect) leaving 833 species. We ran separate analyses for the Indo-pacific and Atlantic oceans (674 species in the Indo-Pacific Ocean and 159 species in the Atlantic Ocean). In addition, we also re-ran the analyses taking only species that are not sensitive to fishing, defined as 50% of the species with the lowest values of the fishing sensitivity index (Cheung, Pitcher, & Pauly, 2005). The results are present in Table S1, and show that our conclusions are robust across species with different sensitivity levels. In all cases, we used fish 'family' as a random effect to account for possible phylogenetic non-independence. Model selection was based on an 'all possible subsets' approach that ranked models by AICc scores ('glmulti' function, 'glmulti' package).

3 | RESULTS

3.1 | Change in abundance across a species range

The different ways to calculate the range centre produced very different range centre estimates. On average, the distance between the *Occupancy* and *Abundance centres* was 1,851 ± 68 km (mean ± *SE*), between the *Geographical* and *Abundance centres* 2,014 ± 60 km and between the *Occupancy* and *Geographical centres* 1,210 ± 43 km.

The relationship between abundance and location within the range varied considerably among species (Figure 3). When using the distance to the *Geographical centre* (Figure 3a) we found that the overall regression slopes did not differ from zero (summary effect sizes of the meta-analysis: slope $= 0.00 \pm 0.01$ (*SE*), $p = 0.10$; slopes were negative for 592 species, significantly negative for 154 species, positive for 620 species and significantly positive for 193 species). However, distance to the *Abundance centre* (Figure 3b) and *Occupancy centre* (Figure 3c) showed overall negative slopes significantly different from zero (slope $= -0.058 \pm 0.008$, $p < 0.0001$; and slope $= -0.056 \pm 0.006$, $p < 0.0001$ respectively), despite a large number of species displaying positive slopes. For the *Occupancy centre*, slopes were negative for 750 species, significantly negative for 274 species, positive for 459 species, and significantly positive for 105 species. For the *Abundance centre*, slopes were negative for 759 species, significantly negative for 284 species, positive for 453 species and significantly positive for 125 species.

These slope estimates were based on double-log scale. Using absolute abundances and the *Occupancy centre* we received a significant slope of −0.05, which means that if a population at a distance of 10 km from the range centre contains 100 individuals a population at a distance of 100 km will contain approximately 89 individuals. Thus, despite an overall small effect size and large variability between species, sites located farther from the *Occupancy* and *Abundance centres* tend to contain fewer individuals.

Distance to *Range margins* displayed overall positive slopes, indicating that abundance decreased towards the range edge (slope $= 0.009 \pm 0.002$, $p < 0.0001$). However, approximately an equal number of species displayed positive and negative slopes, as slopes were negative for 566 species, significantly negative for 133 species, positive for 646 species and significantly positive for 187 species. Analyses for each ocean separately showed similar results (Figure S5).

3.2 | Segmented regression

We used segmented regression to test whether changes in abundance across the range change abruptly between the range core and the range periphery. Of the 1,071 species that could be fitted with

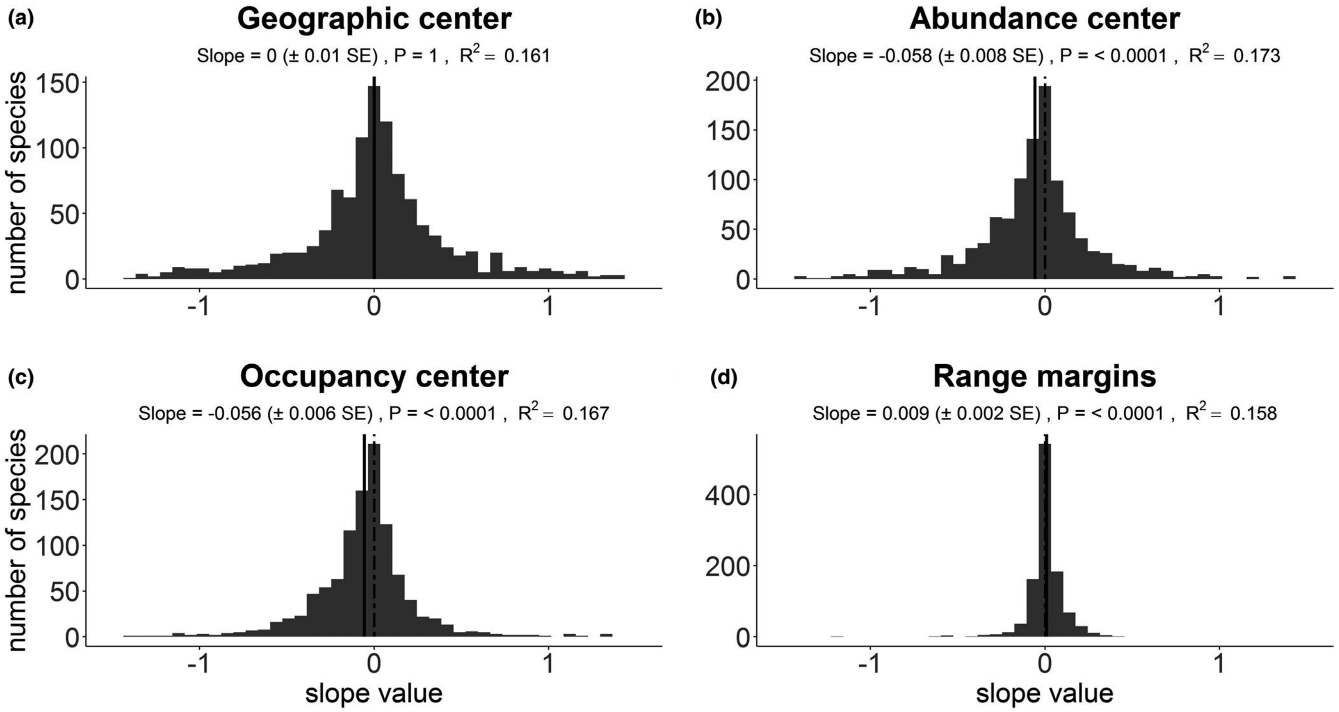

FIGURE 3 The distribution of the regression slopes representing the relationship between abundance and (a-c) distance to the range centres and (d) distance to the range margin. The dashed line is located at zero and the solid line is located at the overall effect size. The 1,076 species presented in the plot are the species with slopes between −1.5 to 1.5 in all four methods

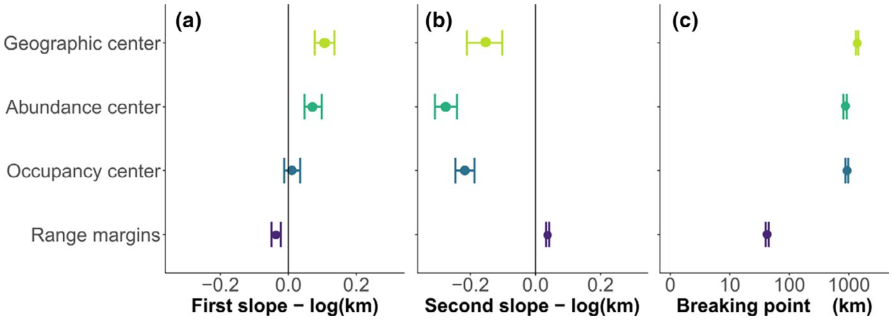

FIGURE 4 Comparison of the segmented regression slopes and the breaking point across the different methods. The slope refers to the relationship between abundance and distance to the range centres in km. (a) First slope represents log-scaled distances across the core of the range. (b) Second slope represents log-scaled distances across the range periphery. (c) The breaking point (km). The plot includes 827 species that fitted the analysis requirements in all four methods. Error bars represent standard errors

a segmented regression (some species were excluded as data limitations prevented the identification of a breakpoint), 308 species displayed a significant difference between the slopes at the core and periphery (using the *Occupancy centre*). Full results of the regressions for all four methods to estimate distance are presented in Table S2.

For the first slope, at the range core, the *Occupancy centre* detected a slope that was not different from zero (0.011 ± 0.02, mean ± *SE*; Figure 4a). The *Abundance centre* and *Geographical centre* displayed a slight positive slope (0.073 ± 0.025 and 0.107 ± 0.029 respectively) and the distance to *Range margins* displayed a slight negative slope (−0.036 ± 0.013). Thus, using these centres, abundance actually slightly increased throughout the range core. However, for the second slope, at the range margins, we found consistent and strong negative slopes for all three centres and a positive slope for distance to *Range margins* (Figure 4b). The results imply that regardless of the way we define range centres, abundance decreases rapidly towards the range margins. Moreover, the use of the segmented model increased the mean R^2 (across species) from 0.167 to 0.220. This increase in explanatory power is even more substantial given that it includes both segments of the regression and is hence is an average of low R^2 for the first segment (with slopes close to zero) and much higher R^2 for the second segment where abundance declines towards the range margins. The segmented regression breaking point represents the point where the slopes change and is around 1,000 (±60 km) from all range centre estimates (Figure 4c). In the alternative method using the distance from the range margins, we found the breaking point to be 50 ± 5 km from the range margin.

3.3 | Grid-based analyses

Worldwide, most of the cells (96%) had an average (across all species in the cell) negative slope (Figure 2b, insert) but the overall effect size was small. We found that latitude was a significant predictor of cell-averaged slopes in three out of five domains, with more negative grid-level slopes at higher latitudes (Table 1). The effect of latitude was similar for the model that accounted for spatial autocorrelations (Table 1). When we rerun the analyses using only cells containing coral reefs (between latitudes of −37.5° and 32°) and adding reef and shallow habitat area as predictors we obtained similar results (Table S3). Distance to the domain centre did not show a clear pattern, as it had significant negative slopes only for the non-spatial model (Table 1), and the slope's sign became positive when adding reef and shallow habitat area as predictors (Table S3).

3.4 | The effect of traits on abundance patterns across species

We used seven ecological and life-history traits to further examine variation in the relationship between abundance and distance from the range centre (Table 2). In the Indo-Pacific Ocean, the best supported models included body size (positive coefficient; Figure 5g), and a small negative effect of fishing sensitivity (negative coefficient, meaning stronger 'abundant centre' patterns as sensitivity increases; Figure 5a). Nevertheless, we note that the four best performing models for the Indo-Pacific have ΔAICc < 2. In the Atlantic Ocean, the best supported model included only mean abundance (negative coefficient, meaning stronger 'abundant centre' patterns as abundance increases; Figure 5d). Figure 5 shows partial residual plots for the effect of the four traits that received the highest support using AICs on the slope of the relationship between abundance and distance to range centre.

4 | DISCUSSION

Although the 'abundant centre' hypothesis has been often assumed, few studies have tested it with samples across the full extent of species ranges and across numerous species (Sagarin & Gaines, 2002b). Two comprehensive recent studies on largely terrestrial organisms found very little support for this hypothesis (Dallas et al., 2017; Santini et al., 2019). However, support for the abundance centre hypothesis in environmental space was found for reef fishes, as species abundances tended to decline at warm or cold temperatures (Waldock et al., 2019). Here, we used data with a global extent and covering 1,215 species of marine fish species and found mixed support for the abundance centre hypothesis. On the one hand, we found high variation among species, meaning that for most species abundance across the range may seem highly stochastic. However, using segmented regressions we also identified a common pattern of separation in abundance-distance relationships between the range core and range margins. Within the range core, we found no consistent pattern of abundance declining with distance. However, towards the range margins we found steep declines in abundance. This has substantial implications for understanding the ecology of species at their range margins.

We were specifically interested in understanding internal variation in abundance within the range. One possibility, implicitly assumed in many tests of the 'abundant centre' hypothesis, is that abundance monotonically changes across the range. This can result in either a constant decline in abundance with distance from the range centre (Figure 1b) or a general lack of a relationship (Figure 1a).

TABLE 1 Grid cell analysis showing the relationship between average cell-level slopes (the mean relationship between abundance and distance to *Occupancy centre* across all species) and distance to the domain centre and to the equator. Significant values are marked in bold. SAR model – simultaneous autoregressive model accounted for spatial autocorrelation

	Distance to domain centre				Distance to equator					
Domain	**Estimate**	***SE***	***t* value**	***p* value**	**Estimate**	***SE***	***t* value**	***p* value**	**R^2**	**Model *p*-value**
All domains model	**$-1.02E^{-07}$**	**$2.76E^{-08}$**	**−3.7**	**0.0003**	**−0.0179**	**0.00601**	**−2.98**	**0.00339**	0.23	**<0.0001**
All domains (SAR model)	$-5.36E^{-08}$	$3.25E^{-08}$	−1.7	0.0995	**−0.0206**	**0.0063**	**−3.26**	**0.001**	0.147	**0.0272**
Indo-Pacific	**$-1.32E^{-07}$**	**$2.75E^{-08}$**	**−4.79**	**<0.0001**	**−0.0332**	**0.00788**	**−4.21**	**<0.0001**	0.308	**<0.0001**
East Pacific	**$8.33E^{-07}$**	**$3.75E^{-07}$**	**2.22**	**0.0411**	−0.0861	0.0408	−2.11	0.0509	0.238	0.114
North-West Atlantic	$9.56E^{-07}$	$4.68E^{-07}$	2.04	0.0685	**−0.0889**	**0.0289**	**−3.08**	**0.0117**	0.609	**0.00912**
East Atlantic	**$-1.60E^{-07}$**	**$5.80E^{-08}$**	**−2.76**	**0.0281**	**0.0189**	**0.00461**	**4.1**	**0.00459**	0.729	**0.0104**
South-West Atlantic	$-9.18E^{-08}$	$3.17E^{-07}$	−0.29	0.779	−0.0129	0.0314	−0.411	0.691	0.224	0.319

TABLE 2 The effect of traits on the abundance-distance slopes. Analyses were conducted separately for each ocean (Indo-Pacific *n* = 674, Atlantic *n* = 159). The table shows the 10 top models with the lowest AIC values, and the regression coefficients for the predictors that were included in the model. Diet was not found in any of the models thus was excluded from the table

Ocean	Intercept	Range size (log10)	Abundance (log10)	Fishing sensitivity	Trophic level	Body size (log10)	Distance to Coral Triangle	Lat.	*df*	logLik	AICc
Indo-Pacific	−0.167	–	–	−0.003	–	0.157	–	–	5	−5.092	20.275
Indo-Pacific	−0.022	–	–	–	–	–	–	–	3	−7.289	20.614
Indo-Pacific	−0.220	0.016	–	–	–	–	–	–	4	−6.658	21.376
Indo-Pacific	−0.342	0.014	–	−0.003	–	0.152	–	–	6	−4.931	21.987
Indo-Pacific	−0.082	–	–	–	–	0.041	–	–	4	−8.037	24.134
Indo-Pacific	−0.269	0.015	–	–	–	0.037	–	–	5	−7.729	25.548
Indo-Pacific	−0.154	–	−0.023	−0.003	–	0.157	–	–	6	−6.927	25.980
Indo-Pacific	−0.013	–	−0.020	–	–	–	–	–	4	−9.606	27.272
Indo-Pacific	−0.321	0.013	−0.018	−0.003	–	0.151	–	–	7	−7.359	28.887
Indo-Pacific	−0.205	0.015	−0.015	–	–	–	–	–	5	−9.452	28.993
Atlantic	0.059	–	−0.216	–	–	–	–	–	4	−76.78	161.82
Atlantic	0.328	–	−0.231	–	−0.077	–	–	–	5	−77.52	165.44
Atlantic	−0.105	–	–	–	–	–	–	–	3	−80.25	166.65
Atlantic	0.136	–	−0.222	–	–	−0.047	–	–	5	−78.16	166.72
Atlantic	−0.407	0.038	−0.235	–	–	–	–	–	5	−78.60	167.60
Atlantic	0.317	–	−0.230	–	−0.079	0.013	–	–	6	−78.97	170.48
Atlantic	−0.123	0.037	−0.249	–	−0.075	–	–	–	6	−79.40	171.36
Atlantic	0.078	–	–	–	−0.055	–	–	–	4	−81.71	171.67
Atlantic	−0.107	–	–	–	–	0.001	–	–	4	−81.77	171.79
Atlantic	−0.006	–	−0.217	–	–	–	–	0.004	5	−80.71	171.82

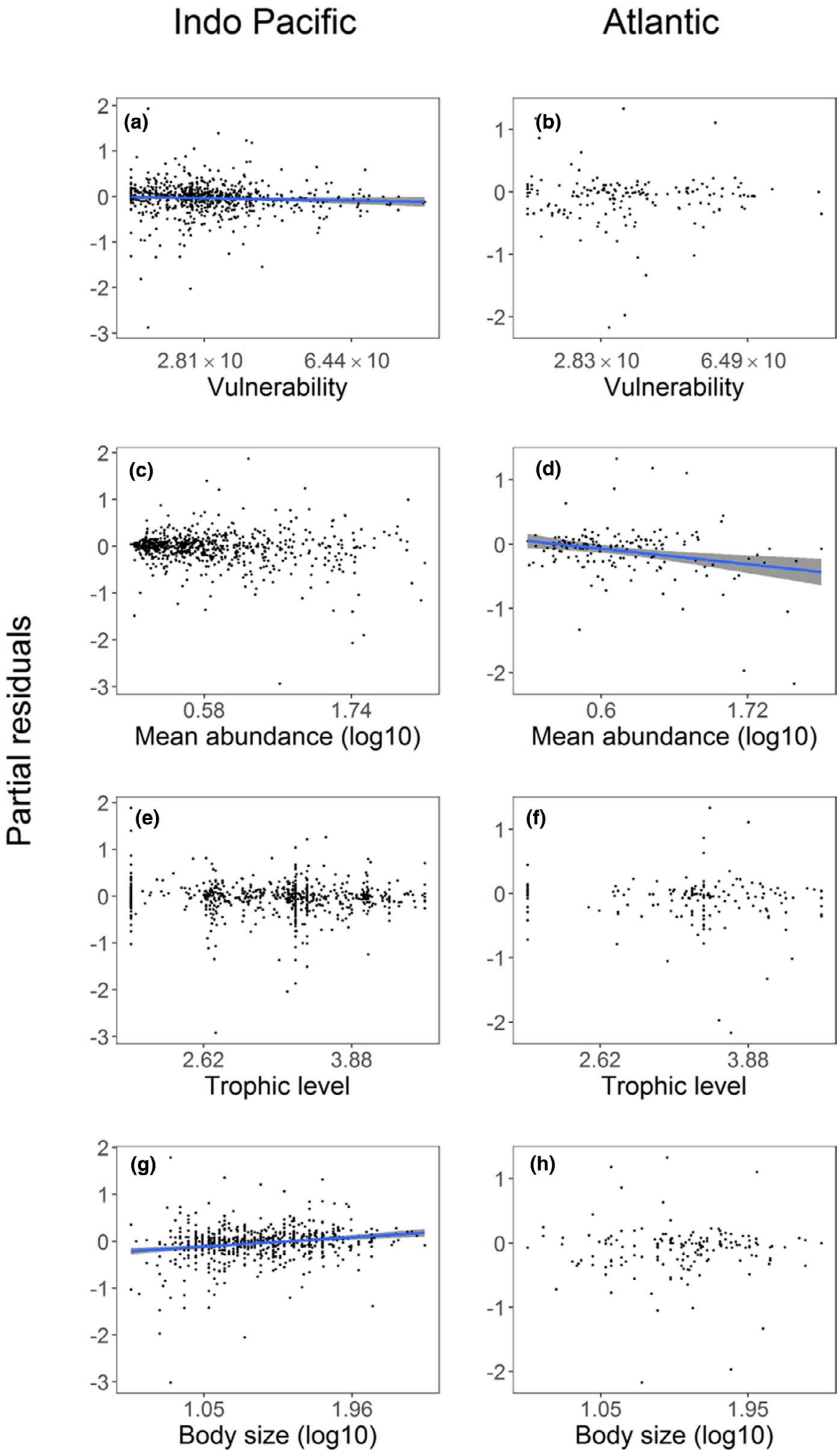

FIGURE 5 Partial residual plot (component + residuals) showing the relationship between species level slopes (representing the relationship between abundance and distance to *Occupancy centre*) and traits. Each dot represents a single species. Plots with trend lines represent traits significantly different from zero

However, by using segmented regressions we were able to test two additional scenarios. The first is that abundance remains high in the range centre and only drops abruptly towards the range margins (Figure 1d). The second, suggests that abundance drops steeply away from the range core and remains constantly low towards the range margins (Figure 1c). Using the *Occupancy centre*, the first slope of the segmented regression did not differ from zero, meaning that we found no directional changes in abundance across the core of species ranges. This suggests that either abundances in the core are stable, or that abundances fluctuate without relation to proximity to the centre of species ranges (Figure 1a). The latter is in line with a pattern coined 'peak and tail' (Mcgill & Collins, 2003), where there are multiple peaks in abundance within the range, but with little predictable variation. Such fluctuation within the core could result from patchy local biotic and abiotic factors shaping small-scale variation in abundance, but also from simple stochasticity.

Using the segmented regressions, we also found significant declines in abundance towards the range margins (similar scenario to Figure 1d). These results indicate that beyond approximately 1,000 km, abundances decline towards the closest range edge, with a mean slope of −0.2. This slope is much steeper than the slope found over the entire range (−0.056). Several mechanisms may produce a steep decrease in abundance towards the range margins. For example in source-sink dynamics (Pulliam, 1988) core populations may live in regions where growth rates are positive and hence population sizes are high, while emigration of individuals out of these core areas maintain small populations towards range margins, despite potential negative growth rates. This is in line with theoretical expectation that central populations should be more stable and resistant to environmental changes as opposed to marginal populations (Guo, Taper, Schoenberger, & Brandle, 2005). Other hypotheses for the decline in abundance towards the range margins include dispersal limitation, that may be independence of the underlying environmental gradient. Finally, particularly steep responses to environmental gradients at the range margins caused, for example, by nonlinear thermal response curves (Waldock et al., 2019), may also cause the steep declines in abundance towards the range margins.

We further compared four different versions of the abundance centre hypothesis. We found that the strongest predictors of abundance are the *Occupancy* and *Abundance centres*. Hence, areas of high occupancy, that presumably reflect species optimal biotic and abiotic environments (Mellin, Bradshaw, Meekan, & Caley, 2010; Mellin et al., 2016), are not necessarily situated in the geographical centre of the distribution (Martínez-Meyer et al., 2013; Pironon et al., 2015). This may be, at least partly, an outcome of the patchy distribution of reef habitats which means that for many species the *Geographical centre* may consist of unsuitable stretches of open ocean.

The exact method to define the range centre had a large effect and thus the definition of the range centre may explain the generally poor fit the of the 'abundant centre' hypothesis to empirical data (Brewer & Gaston, 2002; Defeo & Cardoso, 2004; Gilman, 2005; Hobbs, Jones, Munday, Connolly, & Srinivasan, 2012; Kluth & Bruelheide, 2005; Lima, Ribeiro, Queiroz, Hawkins, & Santos, 2007; Martínez-Meyer et al., 2013; Pironon et al., 2017; Samis & Eckert, 2007). Nevertheless, recent studies have found weak support for systematic changes in abundance regardless of the method used (Dallas et al., 2017; Pironon et al., 2015; Santini et al., 2019). Interestingly, another study on reef fish found clear changes in reef fish abundance with sea surface temperature (Waldock et al., 2019). Thus, it is possible that reef fishes as a group tend to better conform to the 'abundant centre' hypothesis.

We averaged the slopes of all species in 5° × 5° grid cells to provide geographical context to the 'abundant centre' pattern. In general, grid cells farther from the equator contain more negative slopes (Table 1). This suggests that the steep climatic gradients associated with a north-south range orientation may be responsible for the relatively steep changes in abundance with distance from range centres (Waldock et al., 2019). However, we did not detect consistent patterns of change with distance from the domain centres (Table 1, Table S3). This suggests that historic processes and isolation from high diversity centres do not play a strong role in creating abundance gradients within the range (Pironon et al., 2017).

We used life history and ecological traits to examine variation in the fit to the 'abundant centre' pattern, with the slope of the linear association between abundance and distance to *Occupancy centre* as a species-level effect size (Figure 5). For Atlantic species, the variation in slopes was best explained by the mean abundance, and declines in abundance across the range are more likely for species with higher overall abundances. This pattern is likely to be mostly statistical in origin, as the ability to detect a strong negative slope is only possible when abundance is high enough to produce substantial variation in abundance. At the extreme end of the spectrum, for a species only seen as a single individual within transects, we will not be able to detect a gradient in abundance at all. At the same time, these findings suggest that the 'abundant centre' pattern may be more common, and perhaps stronger, than observed here, but frequently overlooked because of the low power of analyses for most (i.e. rare) species. In the Indo-Pacific, the main trait that influenced the strength of the 'abundant centre' pattern was body size. This fits our expectation that large species will display shallower slopes as they are likely to be generally rare everywhere (Brown, Gillooly, Allen, Savage, & West, 2004), and have high dispersal rates. However, we note that body size correlated with many other life-history traits that are hard to separate in macroecological-scale analyses.

Our analyses were based on reefs that are inheritably patchy due to the uneven distribution of hard substrate within the ocean. This patchiness has several implications. Patchiness may impact local abundance estimates when samples are taken outside of patches and hence in sub-optimal habitats. This will cause many abundance estimates to be low and reduce the ability to observe abundance gradients across the range even when they may be present. However, while such patchiness is definitely relevant for reefs imbedded within a larger matrix of unsuitable habitat (e.g. open ocean), this is unlikely to substantially impact our results as sampling was confined to reefs and hence only the relevant habitat for reef fishes was sampled. Patchiness in reef habitat is also likely to impact dispersal among patches and meta-population dynamics, which may impact local abundance estimates. However, whether this reinforces or weakens 'abundant centre' patterns will depend on whether patchiness is more pronounce on the range centre or range margins, and on the exact effect of these dynamics on abundances.

Patchiness in sampling may also cause the range size of species to be underestimated. Nonetheless, as the study extent was global (Figure 1) we expect that for most species we obtained reasonable estimates of the range. For the species assessed by the IUCN (564 out of the 1,215 species in our analysis), we found that for the majority of species (401) convex hull estimates of range size are larger than the IUCN estimates, suggesting that underestimation may not be a major problem. When range size is underestimated, this will mostly impact range-margin estimates which will be particularly relevant for the distance to range margin analyses. However, misidentification of range shape may also cause the estimated geographical centre to differ from the true geographical centre had we had the complete range of species. This may somewhat explain the poor fit of the *Geographical centre* to the data. However, even if we could improve the estimate of the species ranges we feel this is unlikely to strongly impact the *Occupancy centre* results. This is because improving the range boundary estimates may simply increase range extent and add zero abundance estimates at great distances from the *Occupancy centre*. As in the analyses we did not include zeros, this will not impact the slope estimates. In addition, quantile regressions, that should account for biases associated with zero inflation, returned similar results (Figure S3). While it is undeniable that including additional data would be desirable, we have no reasons to believe that improving range size estimates would have changed our conclusions.

The *Occupancy centre* can be criticized, as occupancy may in fact be correlated with abundance. Indeed, several hypotheses have been put forward to explain intraspecific abundance-occupancy associations (Gaston et al., 2000). If sampling efforts are biased, then a species may be recorded from fewer localities when it occurs at low densities producing a positive abundance-occupancy association. However, this was shown to be insufficient to explain observed abundance-occupancy associations (Gaston et al., 2000). Moreover, variation in sampling effort is clearly less relevant in our case where sampling was not targeted at a specific species and hence there is no reason to believe sampling may be associated with areas of high densities of a particular species. Other explanations for the intraspecific abundance-occupancy associations are ecological and related to range position, resource distribution or population dynamics (Borregaard & Rahbek, 2010; Gaston et al., 2000; Heino & Tolonen, 2018). However, these are exactly those processes that are believed to also underlie the 'abundant centre' hypothesis. Hence, for example, source-sink population dynamics may produce both a strong abundance-occupancy association and a clear peak in abundance within the range core. Similarly, environmental gradients of habitat suitability will also produce abundance-occupancy associations in parallel to variation in abundance from the core, were habitat suitability is high, to the margins were habitat suitability is lower. Therefore, not using the *Occupancy centre* as a simple means to estimate the locations in which the biotic and abiotic conditions are most favourable simply because abundance and occupancy can be correlated may remove important ecological information.

5 | CONCLUSIONS

The goal of this study was to test a basic hypothesis in ecology: that species are most abundant at their range centre. Previous studies trying to examine the 'abundant centre' pattern have shown great unexplained variation in the fit to the pattern (Brown et al., 1995; Dallas et al., 2017; Defeo & Cardoso, 2004; Gilman, 2005; Langlois et al., 2012; Pironon et al., 2015; Sagarin & Gaines, 2002a; Santini et al., 2019; Tuya et al., 2008). Using a large dataset with an almost global coverage, we found that the geographical centre of a species is not usually the place where it is the most abundant. Moreover, we corroborate previous studies in finding large unexplained variation in abundance. Nevertheless, we do find support for a general gradient in abundance across species ranges, a core with high abundance and occupancy and lower abundance towards range margins. Specifically, we found that the abundance at the core does not change directionally until reaching a distance of approximately 1,000 km from the *Occupancy centre*, after which abundance declines sharply towards the range margins. Thus, for most species across most of their range, abundance cannot be easily predicted by geographical gradients. Hence, within the core, abundance is either mostly regulated by local scale patchy abiotic and biotic factors, or dominated by stochasticity. However, towards the range margins we do find a predictable, although variable, decrease in abundance. Hence, true peripheral populations are likely to be of low abundance. This makes peripheral populations highly sensitive to extirpation due to both natural and anthropogenic impacts.

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DATA AVAILABILITY STATEMENT

The Reef Life Survey (RLS) dataset is available online (https://reeflifesurvey.com/) and the GASPAR group dataset is deposited on Dryad (https://doi.org/10.5061/dryad.jdfn2z380).

ORCID

Itai Granot https://orcid.org/0000-0002-2168-3440
Alan Friedlander https://orcid.org/0000-0003-4858-006X
Sergio R. Floeter https://orcid.org/0000-0002-3201-6504
Jonathan Belmaker https://orcid.org/0000-0002-5618-7359

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BIOSKETCH

Hagar Yancovitch Shalom is MSc student interested in the macro-ecology of coral reef fishes. Most of her work based on spatial analyses and statistical models in R, although her passion is scientific education and diving in the Red Sea.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX A

TRAITS USED TO ASSESS VARIATION IN ABUNDANCE PATTERNS ACROSS SPECIES

We collected information on ecological and life-history traits for all species and examined whether they explained variation in the 'abundant centre' pattern. These traits included:

1. Mean abundance—species with low abundance on average, will statistically tend to have smaller range of abundances (being bound below by zero) and hence may be less likely to display steep slopes. Mean abundance was calculated using only for the sites where the species was present (i.e. excluding sites within the range in which the species was absent).
2. Range size—we expected species with larger ranges to have shallower slopes for two main reasons. First, large ranges may be an indicator of high dispersal potential (Lester, Ruttenberg, Gaines, & Kinlan, 2007), and high dispersal may cause abundance to be similar across sites. Second, for given variation in abundance species with larger ranges will tend to have shallower slopes. We calculated range size as the size of the convex hull surrounding the sites where the species was found ('areaPolygon' function in 'geosphere' package).
3. Body size—in general, species abundance declines as body size increases, which may lead to shallower slopes (see above). In addition, species with large bodies have generally high dispersal rates (Gaston, Blackburn, & Lawton, 1997), which may also lead to shallower slopes. Conversely, we may expect large bodies species to be long-lived, suggesting potentially more stable population dynamics. This would lead to situations where survival is high enough to partially offset the role of demographic stochasticity and lead to clear 'abundant centre' patterns. Body size for

each species was measured as the maximum length recorded in FishBase (Froese & Pauly, 2000).

4. Diet—diet may influence the abundance-distance relationships in several, hard to predict, ways. For example species feeding on higher trophic levels are predicted to be rare and hence may have shallower slopes (see above). In addition, fish species that feed from patchy food sources, such as corals, may be more likely to be aggregated in space, and hence be locally abundant relative to areas without the resources and thus display steeper slopes compared to species that feed from more evenly distributed resources. We used two indices to estimate diet: food type and trophic levels. Information on food type was based on data compilation by the GASPAR group (Kulbicki et al., 2011) with the seven categories: plankton, sessile invertebrates, mobile invertebrates, macroalgae, turf and microalgae, fishes and omnivores. Trophic levels were based on FishBase (Froese & Pauly, 2000).
5. Fishing sensitivity—the effect of fishing on abundance will depend on the strength and spatial patterns of fishing. In general, if fishing is concentrated on the locations where species are abundant we may expect a relatively even distribution of (low) abundance and hence shallow slopes. However, it may also be possible that for harvested populations low abundance of big individuals is replaced by high abundance of small individuals, complicating the spatial patterns. Finally, due to spatial constraints imposed, for example, by MPAs and distance to human settlements (Maire et al., 2016) fishing may target populations irrespectively of the location within the range. This may reduce the ability to detect spatial patterns in abundance. We used a species-level fishing sensitivity index. This index estimates fishing sensitivity based on life histories characteristics (Cheung et al., 2005), and was extracted from FishBase (Froese & Pauly, 2000).
6. Distance to Coral Triangle—within the Indo-Pacific, the ‘Coral Triangle’ contains relatively large expanses of coral reefs (Bellwood, Hughes, Connolly, & Tanner, 2005) and hence dispersal may result in shallower gradients in abundance. In more isolated peripheral locations, dispersal limitation may act to increase the slope. Distance to Coral Triangle was calculated, in the Indo-Pacific only, as the minimal distance of each range centre to 120° E (Bellwood, 2001; Cowman, Parravicini, Kulbicki, & Floeter, 2017).
7. Latitude—strong climatic gradients presumably influence habitat suitability and may be reflected in steep abundance gradients. As climatic gradients are stronger at high latitudes, species are predicted to show steeper spatial gradients compared to species at low latitudes. Conversely, species may have larger range sizes at higher latitudes (Rapoport's rule) contributing to lower conformity to the ‘abundant centre’ pattern at high latitudes (see point two above). Latitude was expressed as the absolute distance of the range centre to the equator.