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The Shifting Tide: Investigating If Tropical Micro-Tidal Zones Act as Diverse Ecotones with Small-Scale Spatial Diversity Analysis of Ophiuroidea and Echinoidea

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Abstract
Introduction: Biodiversity is not static, and regions with high levels of temporal and spatial variation or ecotones, may be critical for maintaining high biodiversity. The micro-tidal zone or transition from marine to terrestrial environments is a region with high levels of temporal and spatial variation. *Ophiuroidea* and *Echinoidea* have physiological and behavioural adaptions which allow them to be abundant in the micro-tidal zone. There is little research on the diversity of *Ophiuroidea* and *Echinoidea* on small spatial and temporal scales within the micro-tidal zone.
Methods: This study aims to determine the possibility of a micro-tidal zone acting as an ecotone through analysis of *Ophiuroidea* and *Echinoidea* spatial and temporal diversity. Ecological Data was collected along two transects in the micro-tidal zone of Half Moon Caye, Belize. Shannon diversity indices were calculated and used for conditional probabilities to assess biodiversity at various regions in the zone. Statistical analysis was done with the Kruskal-Wallis Test, linear regression, and Chi-square analysis.
Results: Evidence suggests that *A. punctulata* differs from all other species in the distance from high tide, this corresponds to the high conditional probability close to shore compared to other species. A relationship was found between the distance from high tide and both abundance and species richness. *O. appressa* and *E. lucunter* abundance was determined to be dependent of the time of day, but this was independent for all other species.
Discussion: Patterns in biodiversity suggest that the outer region of the micro-tidal zone has a higher species richness due to overlap with species adapted to deeper locations. Furthermore, there is evidence which suggests there may be differences throughout shallower portions of the micro-tidal zone, but further analysis needs to be done with consideration of the physical conditions in this region. In addition to spatial differences, there were differences seen depending on the time of day which may suggest that some species move out of the intertidal zone at night.
Conclusion: This study indicates how the tropical micro-tidal zone may be a critical region acting as an ecotone, providing habitat for a wide range of species on different spatial and temporal scales.

Keywords: ecotones; micro-tidal zones; *Echinoidea*; *Ophiuroidea*; biodiversity; Shannon diversity index

Introduction

When considering preserving the world's ecosystems, biodiversity is a critical point of analysis. Since the early 1990's, a vast amount of evidence has emerged highlighting the importance of biodiversity by depicting its relationship with ecological function [1,2]. Patterns of biodiversity are not constant and are highly variable, both on spatial and temporal scales [3]. Many studies have shown high levels of variance on large spatial scales; however, measurable differences in biodiversity do occur on small spatial scales [4,5]. Ecotones are regions of transition in which one ecosystem coincides with another [6–8]. These ecotones are defined by either physical factors or biotic factors such as regions with cooccurring flora [9,10]. Regardless of the type or number of overlapping variables in an ecotone, the biodiversity tends to be higher, as some species from both adjacent regions can tolerate the conditions in the ecotone [11,12]. Additionally, evidence suggests that the species composition in these ecotones is not static and instead varies with time [13]. Not only are ecotones critical regions for biodiversity, but these regions are being highly affected by changes in the climate. Both global and local changes to abiotic factors can shift the position and size of ecotones [14]. Potentially causing detrimental effects to the species found throughout these ecotones.

Islands are a common physical phenomenon which lead to the formation many ecotones. Beyond the major transition between marine and terrestrial environments, islands also have a considerable number of smaller ecotones [15]. The intertidal zone, a coastline region greatly affected by high and low tide, is a critical ecotone in island environments, although some intertidal zones drastically change between high and low tide, there are some, referred to as micro-tidal zones, which experience less drastic changes [16-19]. Despite this, micro-tidal zones contain a unique set of conditions. In which they differ from other marine environments in factors such as, salinity and alkalinity [20]. In addition to this, there is a high level of wave action which results in physical stress on organisms living in this region. Consequently, many organisms found in micro-tidal zones have the ability to strongly adhere to substrates [21,22]. The extremity of these conditions is variable depending on the location within the micro-tidal zone, thus having large impacts on the species diversity throughout the region.

Benthic invertebrates make up the majority of species found in micro-tidal zones. Echinoderms are a phylum of aquatic invertebrates which are found in a range of environments, one such environment is intertidal zones [23]. Being osmoconformers, echinoderms are highly sensitive to changes in salinity as this directly correlates to changes in their coelomic fluid [24]. There is also evidence emerging which suggests that the adhesive ability of certain species of *Echinoidea* may be influenced by the material to which they adhere [25]. Research into the genetic makeup of a *Ophiuroidea* species suggests that there are habitat-dependent differences between subtidal and intertidal populations [26]. Although, Muths et al. (2006) suggested multiple reasons for this difference in genes, one such suggestion was the need to tolerate conditions in the intertidal zone. This adaption is likely associated with protiens needing to survive desiccation, high temperatures, high salinity, and hypoxia. Evidence suggests many species of echinoderms are nocturnal and increase in visibility at night [27, 28]. Many studies have compared distributions of a single species on small scales or multiple species on large scales. Nevertheless, there is a lack of research into the small-scale spatial diversity of multiple specific specie groups in micro-tidal zones.

This study attempts to survey the spatial trends of echinoderms, in the intertidal zone of Lighthouse Atoll, off the coast of Belize city, Belize. This will be done with consideration of the distance from shore where species are found, to determine if there are trends in terms of small-scale changes and species diversity. Current knowledge on echinoderms, suggests most of the observations will be *Ophiuroidea* and *Echinoidea.* Considering the intertidal zone typically acts as an ecotone, there will likely be differences in overall biodiversity at different distances from the hightide line. However, it is unclear how exactly this transition affects the species diversity of large groups. Given what is known of *Ophiuroidea* and *Echinoidea* and their tolerance to salinity and high wave action it is likely the most diverse region is at relatively far distances from the shore where both these factors are not extreme. In addition to taking distance into account the intertidal zone will be sampled during the day and at night to determine if time of day plays a factor in species diversity of the micro-tidal zone. Although, *Echinoidea* are nocturnal and are typically more visible at night in reef habitats, it is unknown if this will be the case in the micro-tidal zone. There is the possibility that some species may move out of the micro-tidal zone at night, leading to decreased species diversity at this time [27, 28]. *Ophiuroidea* and *Echinoidea* dominate the micro-tidal zone, and understanding the spatial and temporal distribution of these species in is critical as climate change leads to differing conditions throughout this region.

Methods

Field Site

Sampling was done on a small Island, Half Moon Caye, which is located within the lagoon on the Lighthouse Atoll, off the coast of Belize City, Belize (17°12'13.2"N 87°32'05.6"W). This region was first designated as a protected region almost 100 years ago, and since then has become a marine protected area. Additionally, this island is considered a world heritage site by UNESCO. Two transects were selected on the south side of the island, facing the outer edge of the lagoon. The transects started above the high tide line; they were approximately 5 meters apart and 20 meters long. This area of the beach had a shallow region laterally to the shore, forming a shallow pool. This was a rocky area which was relatively calm as well as having more drastic changes between tides compared to the surrounding beach.

Sampling

Sampling was done rapidly, throughout a four-day period in May of 2023 (May 9-12). In total, sampling was done six times, three times around midday and three times at night after the sun had completely set. Rocks of a large enough size which were able to be flipped were searched along both transects. Identification was done visually, by taking pictures, and by the occasional collection of an individual for short periods to ensure specimens were identified correctly. Identification was done with the Reef Creature Identification guide developed by Humann, Deloach, and Wilk in 2013. The distance to the high tide and the current tide was recorded, along with the distance to each species.

Data Analysis

Biodiversity was analyzed using variations of Shannon’s Diversity index [29]. Shannon’s Diversity was calculated globally, and for each species. The diversity of separated regions from the hightide line were then calculated using methods for diversity analysis which were taken from a paper by Gorelick in 2006 [30]. This is done using conditional probabilities, that being the probability of finding a certain species of echinoderm given a specific distance from shore.

$$(i|j) = p_{ij} \cdot \log_2\left(\frac{p_{ij}}{p_i \cdot p_j}\right)$$

Distances were grouped in intervals of 500 centimetres (1=0 to 499 cm, 2=500 to 999 cm, 3= 1000 to 1499 cm, 4= 1500 to 1999 cm, 5= 2000 to 2499 cm, and 6= 2500 to

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2820 cm). Analysis was done to determine if there was a significant difference between each species in terms of the distance from the hightide in which the individuals were found. Both homology of variance and normality could not be confirmed with a Bartlett test (p-value = 0.012) and Shapiro-Wilk test (p-value = 2.267e-08), respectively. Accordingly, the non-parametric Kruskal-Wallis Test was completed in lieu of an analysis of variance. Subsequently, a post hoc pairwise Wilcox analysis was competed to compare each species. The relationship between distance from hightide and overall species abundance and richness was considered with regression analysis. Distances were separated into 2-meter groupings from which the species' abundance and richness were taken. Transformations were made when needed, to determine the relationship with the lowest possible R^2 value. The data was separated by time of day and species and was graphed in ordered to visualize differences on the temporal scale. To remove biases associated with different sample sizes the values were normalized to sample sizes of 100 (divided by total and multiplied by 100). A chi-square test of independence was then completed to determine if there is significant association between the species and time of day. The residuals of this analysis were used to determine which species' abundances differ based on the time of day. For both the Kruskal-Wallis Test and chi-square test species which were in low abundance were omitted.

Results

Only species of *Ophiuroidea* and *Echinoidea* were found, and a variety of both groups were found throughout the micro-tidal zone. In total 15 species were found in the micro-tidal zone including eight species of *Ophiuroidea (Ophiothrix angulata, Ophioderma appressa, Oohiocoma echinata, Ophiderma phoenium, Ophiomyxa flaccida, Ophiocoma paucigranulata, Ophicoma wendtii, Ophionereis reticulata)* and seven species of *Echinoidea (Eucidaris tribulodies, Tripneutstes ventricosus, Arabacia punctulata, Echinometra viridis, Echinometra lucunter, Lytechinus williamsi, and Diadema antillarum).* As expected *Echinoidea* tended to be on top or attached to the underside of rocks. *Ophiuroidea* was mostly found hiding under rocks, however, some species were missed as they burrowed into the sand too quickly to identify.

	1	2	3	4	5	6
O. angulata		0.018	0.013	0.029	0.055	0.090
O. appressa		0.018	0.008	0.043	0.058	0.041
E. tribuloides	0.014	0.008	0.014	0.031	0.023	0.044
O. echinata	0.008	0.011	0.008	0.078	0.029	0.023
E. lucunter		0.005	0.007	0.013	0.017	0.012
A. punctulata		0.045	0.009	0.009	0.003	
O. paucigranulata			0.011	0.025	0.009	0.006
O. reticulata			0.006	0.005		0.017
D. antillarum					0.003	0.009
L. williamsi		0.044	0.006			
E. viridis				0.007		
O. flaccida						0.003
O. phoenium						0.003
O. wendtii						0.003
T. ventricosus						0.003

Figure 1. Analysis of biodiversity of *Ophiuroidea* and *Echinoidea* in the micro-tidal zone of Lighthouse Atoll off the coast of Belize. Species are separated by rows and distances are separated by columns (1 = 0 to 499 cm, 2 = 500 to 999 cm, 3 = 1000 to 1499 cm, 4 = 1500 to 1999 cm, 5 = 2000 to 2499 cm, and 6 = 2500 to 2820 cm). Values represent the conditional probability of finding a given species in a given location, higher probabilities are highlighted with darker shades and lower probabilities with lighter shades.

Conditional probabilities were determined for each species at each distance grouping from hightide (Figure 1). Both *E. tribuloides* and *O. echinata* were found throughout the entire micro-tidal zone. Species that tended to have lower levels of diversity were more commonly found at large distances from the hightide line (Figure 1). In terms of total Shannon's Diversity *O. angulata* was the most abundant of all the echinoderm species seen in the micro-tidal zone but was not found in the whole micro-tidal region. The total biodiversity of *Ophiuroidea* and *Echinoidea* in the micro-tidal zone when analyzed with Shannon's diversity index was determined to be 3.03 (Table 1).

Table 1. The Shannon diversity indices of *Ophiuroidea* and *Echinoidea* species seen in the intertidal zone. Species are ordered from the most common to the least common and the overall value is bolded.

Species	Shannon's Diversity Indices
O. angulata	0.510
O. appressa	0.464
E. tribuloides	0.415
O. echinata	0.365
E. lucunter	0.281
A. punctulata	0.268
O. paucigranulata	0.214
O. reticulata	0.159
D. antillarum	0.075
L. williamsi	0.043
E. viridis	0.024
O. flaccida	0.024
O. phoenium	0.024
O. wendtii	0.024
T. ventricosus	0.024
Total	**3.03**

Table 2. Results of Wilcox pairwise analysis comparing the average distance that *Ophiuroidea* and *Echinoidea* species were found from the hightide line. Species seen less than fifteen times were omitted. Pairs with significant p-values are indicated with **.

Species Pair	P-value
O. appressa-O. angulata	0.73441
O. echinata-O. angulata	0.73957
*A. punctulata -O. angulata***	$3.2x10^{-7}$
E. lucunter-O. angulata	0.23798
E. tribuloides-O. angulata	0.22330
O. echinata - O. appressa	0.91865
A. punctulata - O. appressa **	$1.0x10^{-6}$
E. lucunter- O. appressa	0.33998
E. tribuloides- O. appressa	0.42238
A. punctulata -O. echinata **	$7.8x10^{-7}$
E. lucunter-O. echinata	0.32658
E. tribuloides-O. echinata	0.42238
E. lucunter-A. punctulata **	0.00042
E. tribuloides-A. punctulata **	0.00142
E. tribuloides- E. lucunter	0.91865

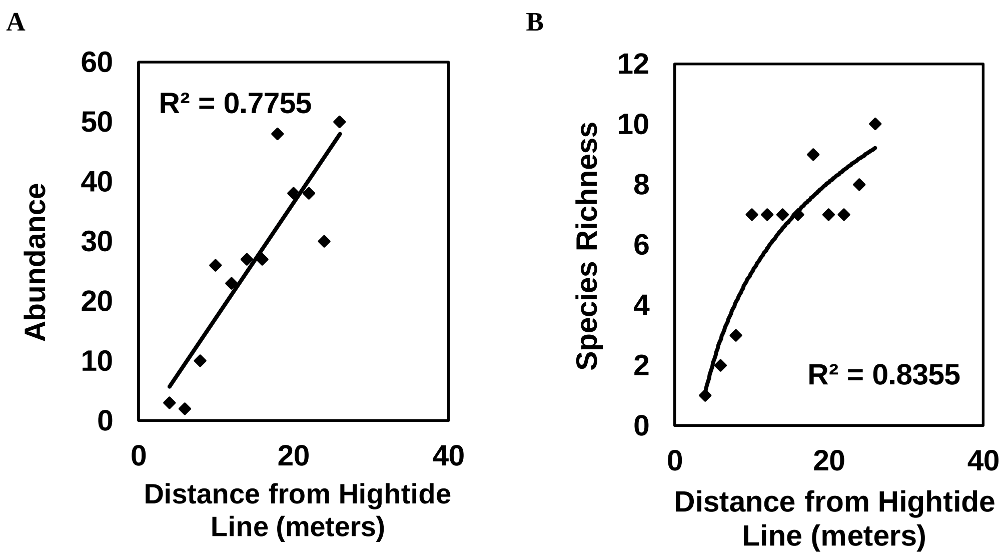

Figure 2. Analysis of trends between the distance from shore and the diversity of *Ophiuroidea* and *Echinoidea* using regression. A) Linear relationship between the abundance of *Ophiuroidea* and *Echinoidea* and the distance. B) Logarithmic transformation of species richness and distance from hightide line, both a linear and logarithmic transformation were assessed. The R^2 values are displayed on the chart, produced using Microsoft Excel.

There is significant evidence suggesting that the average distance from the hightide line differs between species (p-value=$9.072x10^{-7}$). Wilcox pairwise comparisons determined that *A. punctulata* is significantly different from all the other groups (Table 2). There is a relationship between the distance from hightide and both species' abundance and richness. There is a linear relationship between species abundance and distance from the hightide line with 77.6% of the variance in species abundance being explained by the distance from the hightide line (Figure 2A). Additionally, 83.6% of the variance in species richness can be explained by the distance from the hightide line (Figure 2B). Unlike species abundance the relationship between species richness and distance is logarithmic.

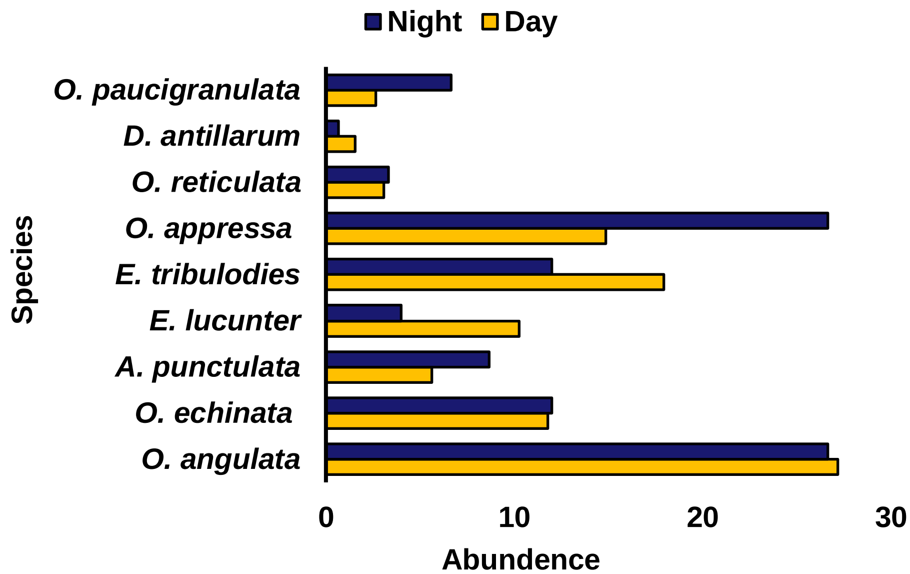

Figure 3. Comparison of species abundance during the day and at night for *Ophiuroidea* and *Echinoidea* in the intertidal zone of an atoll off the coast of Belize. Species only seen on one or two occasions were omitted. The abundance values were corrected for total differences seen during the night and day (by dividing by the total and multiplying by a factor of 100). Produced in Microsoft Excel.

There were 195 individuals seen during the day and 150 individuals seen at night. There is significant evidence suggesting that the recorded species abundance and time of day are not independent (X^2=24.746, p-value= 0.03716). Post hoc analysis determined that only *O. appressa* and *E. lucunter* did not show independence between time of day and species abundance (residuals= ±2.71 and ±2.18 respectively). Interestingly, this difference in recorded species abundance was not consistent with *O. appressa* and *E. lucunter*. *E. lucunter* was seen twice as much during the day compared to at night; opposing this was *O. appressa* being seen almost twice more at night compared to during the day (Figure 3). This is a drastic difference compared to some species such as *O. echinate* and *O. angulata* which were seen at the same rate regardless of the time of day (Figure 3).

Discussion

This study investigated the diversity and distribution of *Ophiuroidea* and *Echinoidea* in the intertidal zone of Lighthouse Atoll in Belize. The trends between the distance from the hightide line and echinoderm diversity was determined using multiple statistical tests. Additionally, differences between species abundance and richness were highlighted. The results from this study demonstrate how differences in species diversity can be seen in small transition regions, which allow for the overlap of species. This follows the concept of ecotones which are ecologically diverse as the in-between conditions allow for the survival of more specializations. Thus, by acting as an ecotone the microtidal zone on Half Moon Caye had relatively high levels of biodiversity, demonstrated through the Shannon diversity index which was on the higher range of what is typically seen in biodiversity analysis. The spatial biodiversity analysis demonstrated how there are differences in biodiversity that correspond to small differences in distance from the shore. Very few species could survive in the range closest to shore, and the number of species rapidly increased after this. However, at further distances from the shore many of these early species are no longer found. Interestingly, many species found at the furthest distances from were only found at those large distances. Of these *O. flaccida* and *T. ventricosus* are commonly found in reefs and seagrass and *O. flaccida* and *O. wendtii* is a burrower and was rarely seen .[29]. *E. tribuloides* and *O. echinata* were the only two species found throughout the entire region of the micro-tidal zone. This suggests that these species can survive in a range of conditions. The highest probability of finding *O. echinata* was in the middle region of the intertidal zone (1500 cm to 1999 cm), with the probabilities decreasing in either direction. This is likely an indication that the conditions in this midzone are optimal for *O. echinata*, nonetheless *O. echinata* can survive fairly well outside of these conditions. This trend was not seen with *E. tribuloides*, as the region which *E. tribuloides* is most likely to be found is the furthest from the hightide line. It is hard to determine exactly what this indicates, but it is possible that *E. tribuloides* is optimized to deeper conditions and is able to survive in the micro-tidal zone. *O. angulata* was the most common species in the micro-tidal zone overall, suggesting this species is either very successful in this region or is very common in general. Strong conclusions on the diversity of these species cannot be made even so, this data does demonstrate small-scale trends in species diversity.

The species abundance increases as the distance from the hightide increases. Even though this relationship is not extremely strong, the variance in species abundance is still largely explained by the distance from hightide. It is not surprising to find that the overall species abundance increases with the distance from shore. Species richness does not follow the same pattern as species abundance. The relationship between species richness and distance from the hightide line is much stronger in a logarithmic function. This is demonstrating how certain species survive better in conditions closer to shore and other species survive better further from shore. The species richness begins to become stable at further distances as some species found at shorter distances are no longer seen. This was corroborated by the analysis of variance as *A. punctulata* has an average distance significantly lower than other species. This implies that *A. punctulata* inhabits regions closer to shore, likely due to some physical factor which differs between these regions. In terms of biodiversity, there is a high probability of finding *A. punctulata* between 500 cm and 999 cm but low probabilities in other sections. This suggests that *A. punctulata* may be specialized to this small region of the intertidal zone which has shallower water but rarely is exposed to air. This could be due to *A. punctulata* being specialized to live in rocky habitats, this species may have stronger adhesive abilities allowing it to survive in shallower regions with increased wave action [32].

Across all species there were more individuals seen during the day compared to at night. It is possible this large difference in abundance seen may just be due to sampling bias; however, when correcting for this difference there are still notable inconsistencies between certain species during the day and at night. *E. lucunter* was seen much more during the day than at night, likely because they have moved from their protected locations to forage. This is supported by previous evidence which suggests that urchins hunt at night [33]. Yet it is unknown if *E. lucunter* was seen less due to no longer being adhered to rocks or if *E. lucunter* has moved out of the micro-tidal zone in search for food. Other recent studies done on *E. lucunter* found that in regions with higher wave action *E. lucunter* was found under rocks in more protected regions which could explain the large contrast between night and day compared to other species [34]. *O. appressa* was seen much more often at night. It is possible that *O. appressa* is more active at night but there is also the possibility that *O. appressa* was retreating faster during the day due to the exposure to light. Recent evidence has shown that brittle stars have photoreceptors and are able to respond to light [35]. Species to species difference seen across night and day demonstrate the temporal variation in species diversity and highlights the small-scale changes which occur in micro-tidal zones.

Conclusions

This study demonstrates the possibility of measurable differences in *Ophiuroidea* and *Echinoidea* diversity on small spatial and temporal scales in the micro-tidal zone. In doing so, demonstrating how this tropical micro-tidal zone is likely an ecotone and may be critical in terms of larger ecosystem functions. One major downfall of this study is the small sample size, due to the limited sampling time. Still, this study was able to identify and pose interesting questions about ecotone regions such as micro-tidal zones. Species adapted to deeper water being present along the edge of the microtidal zone demonstrates the phenomenon of transition regions supporting a higher number of species which can tolerate intermediate conditions. It would be interesting to continue with this analysis to determine how substantial this effect is across different phyla, and in different landscapes. Additionally, it would be interesting to consider factors such as substrate type, water temperature, salinity, and wave turbulence at various distances from shore in the intertidal zone. With consideration of human impact, it may also be interesting to compare this biodiversity to shorelines which are not protected and have higher levels of human traffic. Knowing how these specialized transition habitats support larger ecosystems is hugely important in terms of knowing what areas to conserve and restore. More research is needed to fully understand the changes that can be made to increase ecosystem functioning by maintaining these critical environments.

Conflicts of Interest

The author declare that they have no conflict of interests.

Ethics Approval and/or Participant Consent

This study was done as part of the Ontario Universities Program in Field Biology – OUPFB and therefore did not require specific ethical approval.

Authors' Contributions

SD: Made contributions to the design of the study, acquisition of the data, mode of analysis, drafting and revising of the work, and final approval of publication.

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