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Quantifying the *in situ* 3-dimensional structural complexity of mangrove tree root systems: Biotic and abiotic implications at the microhabitat scale

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ABSTRACT

The structural complexity of mangrove root systems provides multifunctional ecological habitats that enhance ecosystem processes and ensure the provision of services. To date, the ecological implications and roles of these microstructures at fine scales are overlooked. Here, the complexity among the root systems of three mangrove tree species; Rhizophora mucronata, Avicennia marina and Bruguiera gymnorhiza at two mangrove forests in South Africa, was empirically assessed using 3D scanning techniques to address the biotic and abiotic implications of such structures relative to the occurrence of marine larval communities within the system. Complexity was assessed using three metrics from 3D models: fractal dimension D, the area-volume (AVR) ratio index and Blender interstitial volume. Results indicated that fractal dimensions are not good parameters to determine the structural complexity of mangrove root systems due to the insensitivity to detect differences in the spatial patterns of visibly distinct structures. Additionally, A. marina is the most complex in the AVR index and least for interstitial space, while the inverse is true for R. mucronata. Measuring the comparative complexity of these indices could be advantageous for approximating how boundary layer dynamics change at alternate states of the tide for larval transport and inorganic particle retention (AVR) and providing refuge for organisms while avoiding predators who are too large to navigate among the intricate structures (interstitial space). The incorporation of these metrics at relevant scales is therefore crucial to understand how fine-scale habitat complexity emerges to drive ecosystem services that regulate organic and inorganic cycles and provide multifunctional habitats to ecologically and commercially important taxa.

1. Introduction

The structural complexity of available habitat generally influences biological community organisation by promoting species coexistence through reducing niche overlap (Kremer and Klausmeier, 2013; Levins, 1979), mediating predation by providing refuge for smaller organisms and altering the physical environment (Granek and Frasier, 2007; Nagelkerken, 2009). These effects have been observed in both terrestrial (e.g. Tews et al., 2004; Finke and Denno, 2006) and aquatic systems (e.g. Hindell and Jenkins, 2004; Jenkins et al., 1997). The complexity of self-organising aquatic habitats has been estimated using a variety of tools over varying spatial extents (for a review see Kovalenko et al., 2012). The stride in technological advancement in recent years has enabled the fractal dimensions of objects to be used in 3D space via tomography (e.g.

Perret et al., 2003), photogrammetry (e.g. Fukunaga et al., 2019) and 3D scanning (e.g. Kamal et al., 2017; Reichert et al., 2017). These 3D models, developed using mathematical equations to calculate fractal dimensions of objects to measure non-integer complexity, have been increasingly used to address current ecological issues such as the quantification of coral reef habitat complexity, sediment accretion in mangroves and implications of artificial structures for fish assemblages (Kamal et al., 2017; Porter et al., 2018; Reichert et al., 2017).

The complexity provided by mangrove root systems provides a critical nursery habitat for numerous species of ecological and commercial importance (Nagelkerken, 2009; Rönnbäck et al., 1999). Mangroves also act as a natural filter for pollutants (Kristensen et al., 2011), serve as both a source and sink for nutrients and sediment (Donato et al., 2011), as well as play a pivotal role in protecting coastal communities

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from storm surges (Blankespoor et al., 2017). Only one study (Kamal et al., 2017), however, has made use of realistic quantitative measures to explore the complexity-service dynamics, whilst simple mimics using PVC piping and artificial units of the actual habitat have otherwise been used to evaluate the role of root attributes in attracting juvenile fish (Nagelkerken et al., 2010). Despite the well-documented link between large-scale mangrove habitat complexity and provision of ecosystem services, no information is available on how the fine-scale structural 3D habitat complexity of root systems from different mangrove tree species may help explain the biotic organisation of larval communities.

This study aimed to fill this gap and assessed the in situ structural complexity of three mangrove tree species' root systems; Rhizophora mucronata, Avicennia marina and Bruguiera gymnorhiza at a microhabitat volumetric level of 1 m³. This was done using a low-cost 3D scanning technique developed by Kamal et al. (2014) to produce realistic models of microhabitat level complexity. Additionally, fractal dimensions and traditional complexity measures such as the area-volume ratio (AVR) index and interstitial volume were quantified to compare with the 3D models to provide a holistic estimation of shape, irregularity pattern, self-similarity of the mangrove root systems. In order to refine the role of habitat complexity and its ecological implications, these indices were used as indicators to infer possible enhancing effects of physical characteristics in natural 3D mangrove roots for subsequent usage by recently spawned or recruiting larvae within the mangrove microhabitats. Here, we predict that the values of all indices and their ecological importance significantly differs among the morphologically distinct mangrove root structures of the three species, under the assumption that not all mangrove tree species are equal in their contribution to ecological processes, but play different roles informed by their spatially explicit structural arrangement.

2. Materials and methods

2.1. Study area

Two mangrove forests, situated on the east coast of South Africa, were sampled during October 2018 to determine the structural metrics of the mangrove tree species' root complexity (Fig. 1). At the Mlalazi Estuary (28°57'15' S, 31°46'33' E), the mangrove area is composed of a large number of stands of *B. gymnorhiza* that commonly develops knee roots, but also short, prop-like aerial roots tightly arranged at the base of the stem along river banks and A. marina characterised by thin, pencillike roots that extend from the soil, but grow only to a length of 50 cm (Tomlinson, 1986). There are also patches of R. mucronata, forming a small stand on the banks along the creeks within the forest, with branching roots that derive directly from the trunk of the tree and grow down towards the soil (Peer et al., 2018; Tomlinson, 1986). The Mngazana mangrove forest (31°42"S, 29°25" E) hosts one of the most southerly mangrove forests in the world (Quisthoudt et al., 2013). This mangrove forest has the largest stand of R. mucronata in the country and is dominated by A. marina in terms of percentage coverage followed by B. gymnorhiza (Peer et al., 2018; Rajkaran et al., 2004).

2.2. 3D scanning and model construction

The root systems of selected mangrove tree species were reconstructed as full 3D models to infer their structural complexity using a simple, cost-effective 3D scanning and reconstruction methodology. Adult trees of *A. marina*, *B. gymnorhiza* and *R. mucronata* were identified for scanning at each sampling area, when present. Three haphazard 1x1 m^2 patches of each species' (*A. marina* and *B. gymnorhiza* at Mlalazi and *A. marina* and *R. mucronata* at Mngazana) above-ground roots were identified and scanned using the technique developed by Kamal et al. (2014). This technique involves using an Xbox Kinect V2 for windows sensor, connected to a HP 450 G4 probook, powered by an inverter and 12 V battery for use in the field. During each scan, the Kinect sensor was



Fig. 1. Map of study area indicating the habitats where root systems of different tree species were scanned (O) for resultant complexity 3D models in Mlalazi (top) and Mngazana (bottom) on the east coast of South Africa.

carefully moved in a sine shape above the root system whilst changing the pitch and rolling angle to capture the full 360° around the root system of interest. Due to hardware limitations, the scanning parameters were set at 256^3 voxel m⁻³ resolution where each voxel is equivalent to 4 mm and saved as a Wavefront file (.obj). As suggested by Kamal et al. (2014), scans were usually conducted at low tide during dusk to minimise interference (holes in the resulting 3D mesh) due to temperature differences, moisture or sunlight exposure effects. The advantage of using this method is that it is cost-effective, simple and produces rapid real-time images in order to assess the completeness of the resulting 3D model *in situ*.

Raw 3D models (.obj files) (Fig. 2a–c) for each patch were imported and visualised in Blender v2.8 (open source 3D software; www.blender. org/features/). Errors in the original 3D models were corrected by deleting minor holes (<15 mm), duplicates of surfaces, non-manifold edges and unwanted objects mistakenly recorded in the mesh to produce a 'clean, watertight' mesh of the 3D models (Fig. 2d–f). The models were then positioned so that the substrate captured in the scan was aligned to the x-axis of the box frame. The resulting 3D models were then exported as Wavefront .obj files for subsequent analysis.

The fractal dimension *D* of the 3D models was calculated from the Wavefront .obj files based on the Bouligand-Minkowski method, using the freely available Bouligand-Minkowski 3D-Toolbox (https://www.facom.ufu.br/~backes/mink3d.html). The Bouligand-Minkowski method is based on the influence volume of an object computed from its dilation, where the fractal dimension can be estimated as:

$$D = 3 - \lim_{r \to 0} \frac{\log(V(r))}{\log(r)} \tag{1}$$

Where V(r) is the influence volume of the object after the dilation process and r is the dilation radius used in the model and corresponds to an absolute value of 1 which is equal to the resolution of the mesh in the 3D model (4 mm for this study) (Florindo et al., 2015). The fractal dimension *D* was then calculated for each model with a dilation radii of 3–20 (r



Fig. 2. Examples of the raw 3D models of mangrove tree species' root systems (a-c), cleaned meshes (d-f) and the 'shrinkwrap tool' (g-i) used in order to estimate the Blender interstitial volume for *R. mucronata* (left), *A. marina* (middle) and *B. gymnorhiza* (right).

 $= \{i \in \mathbb{Z} \mid 3 \le i \le 20\}$). The Bouligand-Minkowski method is considered the most accurate method for calculating fractal dimensions of objects due to its rotational invariance and sensitivity to fine scale structural changes in models (Backes et al., 2009; Reichert et al., 2017; Backes et al., 2010; Tricot, 1995).

Two additional traditional complexity metrics were estimated for each 3D model for comparison with the fractal dimension D analysis. The area-volume ratio (AVR) index is an extension of the rugosity index in 3D space (Kamal et al., 2017) and links the area covered by the model in relation to the volume of the model to its maximum extent within its box frame. The AVR index was computed from each 3D model using the 'Print 3D toolbox' add-on in Blender v2.8, which readily computes the values of surface area and volume of the model. The Blender interstitial volume is defined as the total amount of volumetric space of interstitial gaps of an object and was calculated on each 3D model using the 'shrinkwrap' modifier tool in Blender v2.8 as outlined in detail in Sadchatheeswaran et al. (2019) (Fig. 2h-i). The model was 'wrapped' using the 'shrinkwrap' modifier tool, whereby the volume of the 'shrinkwrapped' model is computed. The difference in the volume of the solid model was calculated using the 'Print 3D toolbox' and the volume of the 'shrink-wrapped' model was calculated to obtain the 'Blender interstitial volume'. Lastly, the surface areas of interstitial gaps of each 3D model were measured on a subset X, Y and Z axes of the model of interest (0.5 m² on the X, Y axes up to its maximum extent on the Z axis) to determine the variability in interstitial gaps of the relative root systems.

2.3. Statistical analysis

All measures of complexity were tested for the assumptions of normality and homogeneity using Shapiro-Wilk and Levene's test respectively. To compare the fractal dimension D among individual 3D models, an ANCOVA, using the log-radius (log (r)) as a covariate and individual model as a fixed factor was performed. Thereafter, Benjamini-Hochberg adjusted pairwise t-tests were used to account for multiple testing (Benjamini and Hochberg, 1995). Interspecific differences among tree species in relation to the complexity measures were analysed with separate 1-way ANOVAs and, significant differences among species were further explored using pairwise t-tests. To assess the variability of the surface area of interstitial gaps, the R package cvequality (Marwick and Krishnamoorthy, 2019) was used to test for significant differences in the coefficient of variation (C_v) among species using the modified signed-likelihood ratio test (M-SLRT) (Krishnamoorthy and Lee, 2014). The relationship among all complexity measures were explored using Pearson's correlations. All statistical tests were carried out in the R environment for computing statistics (R v3.3.1) (R Core Team, 2020) using the vegan (Oksanen et al., 2018) and car (Fox et al., 2018) packages.

3. Results

All 3D models were scanned successfully with minor holes in some

scans due to moisture of the soil that compromised the ability of the RGB-D sensor to effectively close holes at the base of the roots considered. At the 256^3 voxel m⁻³ resolution, the tips of the *A. marina* pneumatophores were systematically slightly truncated and, in cases where the pneumatophores were tightly spaced together and overgrown with algae, they appeared fused at the base. The diameter of the pneumatophores also appeared larger in the scans due to the epiphytic algae that colonised the surface of these roots.

There were significant differences among the log–log slopes of influence volume as a function of dilation radii (ANCOVA, $F_{(11, 3912)} = 1965.5$, p < 0.001; Fig. 3). Furthermore, pairwise tests indicated significant differences (p < 0.05) among all models except between models *A. marina* S1 (MG) and S3 (MG) (p = 0.93) and models *A. marina* S1 (ML) and S3 (ML) (p = 0.123). Models *B. gymnorhiza* S1 (ML) and S2 (ML) (p = 0.14), and *B. gymnorhiza* S2 (ML) and S3 (ML) (p = 0.06) also did not differ in their slopes (Fig. 3).

Overall, AVR index ranged from 0.72 to 2.66 cm⁻¹, with *A. marina* exhibiting the largest (2.3 ± 0.39) and *B. gymnorhiza* the smallest (0.93 ± 0.08) AVR index from Mlalazi. Blender interstitial volume laid between 41.31 and 502 cm³, *R. mucronata* (424.46 \pm 103.75 cm³) and *A. marina* from Mlalazi (155.40 \pm 98.83 cm³) had the highest and lowest mean values, respectively. Fractal dimension *D* ranged from 2.02 to 2.31, with the most complex root system on average being that of *B. gymnorhiza* (2.26 \pm 0.02) and the least complex being *R. mucronata* (2.08 \pm 0.06).

Values for the AVR index, Blender interstitial volume and fractal dimension *D* were normally distributed and homoscedastic. There were significant differences among mangrove root systems that derived from different species in the AVR index (ANOVA, $F_{(3,9)} = 1.103$, p < 0.001; Fig. 4a) and Blender interstitial volume (ANOVA, $F_{(3,9)} = 7.113$, p = 0.002; Fig. 4b). Furthermore, the variability in the surface area of interstitial gaps differed significantly among species ($C_v = 9.332$, p = 0.025; Fig. 4d). Pairwise t-tests indicated that for the AVR index all species were significantly different (p < 0.05) from each other except between *R. mucronata* with *B. gymnorhiza* (p = 0.264) and *A. marina* from Mngazana (p = 0.023). Post-hoc tests for the Blender interstitial volume indicated significantly higher values for *R. mucronata* than *B. gymnorhiza* (p = 0.023) and *A. marina* from both Mngazana (p = 0.007) and Mlalazi (p = 0.003). No differences were observed in fractal dimension *D* (ANOVA, $F_{(3,9)} = 2.716$, p = 0.115; Fig. 4c) and only the

AVR index was significantly correlated with interstitial volume (Fig. 5).

4. Discussion

Interspecific differences of the traditional metrics (AVR index, Blender interstitial volume and interstital gap variability) indicated the unique complexity of the root systems of the three species of mangrove trees examined. The AVR index quantified that the pneumatophores of A. marina are more complex than R. mucronata and B. gymnorhiza, and R. mucronata is slightly more complex than B. gymnorhiza, but not significantly so. The measures on the Blender interstitial volumes and surface area of interstitial gaps indicated that there is more available space with greater interstitial gap variability within the root system of R. mucronata than the other two mangrove tree species. While B. gymnorhiza and R. mucronata differed in interstitial volume, there were no interspecific differences in fractal dimension D. Similarity in the fractal dimension D of A. marina and R. mucronata and the larger interstitial spacing within the root systems of R. mucronata than A. marina matches previous work (Kamal et al., 2014). Some of these findings however contradict those of Kamal et al. (2014) who observed R. mucronata to have a larger AVR than A. marina. The morphological traits that result in the comparative interspecific structural complexity of mangrove tree root systems reflect the interaction between genetic background and the environmental context it faces (Reichert et al., 2017). In this study, complexity differed according to mangrove tree species based on individual models and further intraspecific differences in the log-log slope of dilation radius to influence volume. Intraspecific variability in complexity using photogrammetry techniques has previously been highlighted among quadrats of pneumatophores of A. marina (Beck, 1998). Such individual differences could be a result of the natural variability in the root system of individual trees, which largely depends on the number of roots, distribution and density of pneumatophores, the height and number of branching roots from the stem of R. mucronata and the number of aerial roots extruding from the base of the stem of B. gymnorhiza (Kathiresan and Bingham, 2001).

The results of the AVR index follow the general assumption that smaller organisms/objects have a larger surface area to volume ratio, as observed for *A. marina* and *R. mucronata* (Vogel, 1988). Specific to the arrangement of objects in 3D space, the AVR index has an inverse relationship with the interstitial space amongst its roots (this study). The



Fig. 3. Log-log plot of influence volume as a function of dilation radii calculated from the Bouligand-Minkowski method to estimate the fractal dimension *D* of each 3D model (S1, S2, S3) of the root systems of *R. mucronata, A. marina* and *B. gymnorhiza*. Brackets indicate the site at which the models were scanned, (ML) Mlalazi and (MG) Mngazana.



Fig. 4. Box-plots of species-specific measures of (a) AVR index, (b) Blender interstitial volume, (c) fractal dimension *D* and interstitial gap size (d). The lower and upper limits of each box represent the 25 and 75% percentiles; the horizontal line indicates the median, the vertical lines of each box indicate 1.5x above and below the interquartile range. Letters above each plot indicate homogenous groups derived from multiple pairwise t-tests (p < 0.05), where available. ns, not significant; ***p < 0.001; **p < 0.01; **p < 0.01; **p < 0.05.





horizontal and vertical size of the individual root systems influence the spatial complexity indices measured for all tree species. Differences in the arrangement, compactness and height to which roots grow above the soil can therefore account for the difference in AVR index as well the Blender interstitial volumes within the root systems of the species examined. The seemingly geometrically dissimilar pneumatophores and stilt roots did not differ in terms of fractal dimension and this could be because this metric analyses the irregularity pattern of the model and is quantified in terms of space-occupation and self-similarity. Fractal dimension analysis has been subject to methodological scrutiny and applicability in ecology, because natural objects with distinct morphologies as seen in this study, can have similar fractal dimensions since the fractals of natural 3-dimensional objects vary over very narrow ranges (Halley et al., 2004). Similar methodological limitations have been observed in the quantification of complexity in coral morphology, where fractal dimensions miss certain characteristics such as branching (Reichert et al., 2017). Fractal dimensions may therefore not be the best candidate for empirical assessment of complexity among mangrove root systems at the resolution examined here. Nevertheless, fractal dimensions could prove to be useful at higher resolutions incorporating multiscale fractal dimensions to reduce the loss of information when fractal dimension is synthesised into an absolute value (D) (De Oliveira Plotze et al., 2005; Simberloff et al., 1987). The Blender interstitial volume is best suited to infer how mobile organisms may utilise the space allocation provisioned by the complexity of the habitat structures. Alternatively, the AVR index seems best equipped to determine how the root structures might alter the physical environment to benefit sedimentation, wave dissipation, the colonisation of their surfaces and

passive particle distribution through a net change in fluid dynamics resulting in increased areas of stagnation. Both of these metrics are readily available in 3D software programs such as Blender and are best used in unison for a holistic measure of complexity for ecological interpretation.

The increased volume and variability of interstitial spaces within the roots of R. mucronata may be more advantageous for sheltering diverse mobile organisms who are able to navigate through the narrow gaps to avoid larger predators (Morton, 1990; Rönnbäck et al., 1999; Granek and Frasier, 2007; Nagelkerken et al., 2000; Nagelkerken, 2009). The scales at which these complex habitats operate hence become important depending on the size of the organisms that are able to exploit them. The increment of open spaces will allow organisms such as planktivorous fish to navigate and feed whilst they are within the microhabitat, therefore larvae will be more protected in areas where they are able to fit and move freely, that are inaccessible for large organisms that feed on them (Porter et al., 2018). The enlarged AVR of particular root systems may allow for colonisation of epiphytic biota and thus amplify the amount of food available to primary consumers which is recognised as an attractant for organisms that utilise microhabitats (Verweij et al., 2006). The utilisation and interpretation of complexity and its relation to habitat use is therefore dependent on the scale at which the organism of interest experiences its environment as well as species-specific characteristics such as shape, size and feeding habits (Cocheret De La Morinière et al., 2004).

The complexity of the mangrove roots also alters the physical environment with which it interacts (Kamal et al., 2017; Kathiresan, 2014; Krauss et al., 2003). In this specific context, pneumatophores of A. marina are more complex (as AVR) than R. mucronata, but their ability to dissipate and absorb wave energy will further depend on the aboveground height and biomass of the roots and the depth of the water that flows through these structures (Srikanth et al., 2016). It is thus expected, that at low water levels of ebbing or flooding tides, A. marina might be more effective at changing the pressure and flow characteristics of water. Alternatively, while during storm surges and high tide, R. mucronata might offer protection against high water velocities. The reduction of tidal flow by complexity of root structures also influences passive particle aggregation and sedimentation within mangrove forests (Furukawa et al., 1997; Furukawa and Wolanski, 1996). These areas of particle aggregation driven by changes in boundary layer dynamics may benefit larval retention in areas of reduced flow and sedentary suspension-feeding organisms by facilitating increased ingestion of suspended particles (Lim et al., 2020). Such retentive mechanisms would generally be considered positive, however, complex habitat may also disproportionately aggregate microplastics over their surfaces, acting as sinks of contaminants and hence increasing the risk of ingestion of anthropogenic waste for filter feeding individuals occurring within these habitats (Lim et al., 2020).

Habitat structural complexity through the compartmentalisation of microhabitats within mangrove forests provides linkages among ontogenetic stages of both invertebrates and fish, hence it should be more critically assessed through quantitative empirical information for effective biodiversity and conservation management strategies (Kovalenko et al., 2012). Mangroves have been highlighted as one of the most important ecosystems that contribute to both human and environmental well-being, but are declining at a rapid rate of 1-3% per year (Friess et al., 2019). Efforts for mangrove rehabilitation have largely focused on planting of monospecific stands of Rhizophora spp. with a relatively low success rate in the reestablishment of the forest, fauna and functionality (Cormier-Salem and Panfili, 2016; Lewis et al., 2019; Primavera and Esteban, 2008). The structural diversity of mangrove tree species' root systems shown here likely supports diverse early stage communities as a consequence of larval body size relative to the volume of interstitial space offered within a specific microhabitat (Holling, 1992). In such context, the protection of natural mangrove forests should be prioritised over rehabilitation due to the nuances in fine scale processes of assorted

habitat provided by root diversity that have an impact on the overall functioning of the ecosystem.

The accuracy of the results obtained through traditional complexity and fractal analyses are only as good as the underlying 3D models used and could thus be limited in their precision if the hardware used (3D scanners and laptops) do not meet the technical specifications for the desired model. Thus, scanning objects of interest at fine resolution becomes important in order to get a full model devoid of holes in the resultant mesh. Environmental conditions may also be limiting in producing high quality 3D models as differences in surface temperature and moisture effects may create holes in the mesh. In situ scans of habitats should therefore be carried out in low light and dry, low tide conditions. Limitations withstanding, the complexity measures obtained here using a non-invasive 3D scanning technique could be applicable in intertidal, semi-terrestrial and terrestrial settings with habitat-specific modifications. Complexity of semi-terrestrial habitats has been measured using manual methods that only extend up to 2.5D (Risk, 1972; Young et al., 2017). By incorporating 3D scanning and modelling with the calculation of the fractal dimensions, AVR, Blender interstitial volume and variability in interstitial gap size, into the complexity-dynamics framework, data on the available space within crevices, gullies and exposed macrophytes can be accurately quantified during low tide to complement surface rugosity measures by extension into 3D space. Here, three replicates of three mangrove species' root system at each site were used to test for generic differences in their structural complexity. Given the high intraspecific variability observed, in future, the sample size and number of mangrove species examined should be increased to develop a more robust dataset, as to further characterise the structural complexity among and within species.

Overall, the present study showed that fractal dimensions are suboptimal to quantify the differences in complexity of visibly distinct root structures. The interstitial spaces on their own within root systems might be best suited to discern how larvae and other aquatic organisms interact with microhabitats provided by the roots, while the actual structures might be more useful to infer how they affect fluid and particle dynamics that benefit larval retention and sediment accretion. When used in unison, both of these metrics can provide a holistic measure and subsequent interpretation of ecological implications and should therefore be considered when exploring complexity-service dynamics of mangrove root systems in a context of conservation management.

Authors contributions

LDV, FP and PP conceptualised the study; LDV and FP designed the research; LDV and FP collected the data; LDV analysed the data, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

The data generated herein is available at https://osf.io/a92tm/ view_only=54408a83f6b24770a686cb8292fe1800.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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