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Letter to the editor Open Access

Three-dimensional assessment of movement patterns of Sichuan snub-nosed monkeys affected by habitat structure in temperate forests

DEAR EDITOR,

Movement patterns can reflect species-specific characteristics of individuals and animal groups at a given scale. Accurate three-dimensional (3D) assessment can quantify the relationship between movement patterns of an animal and its unique habitat. Here, we evaluated the effects of habitat structure on movement patterns of the golden snub-nosed monkey (*Rhinopithecus roxellana*). We used airborne light detection and ranging (LiDAR) to map the 3D structure of the temperate forest in the Qinling Mountains (Shaanxi, China). We then integrated field observations of monkey movements with the 3D structure data to characterize movement patterns and habitat use in the horizontal and vertical dimensions. Our analysis revealed that food availability and thermal regulation were the main drivers of movement; however, forest structure and environmental variables affected movement capacity in different age and sex groups. High-canopy forests were associated with increased continuity of movement trajectories and provided habitats with higher food availability, as well as sites favorable for thermal regulation and predation avoidance. The high-resolution 3D forest structure data provided new insights into variation in habitat selection among age and sex groups, which likely reflect sexual dimorphism and the different roles and ranks of individuals. Reconstructing the 3D environment in ecological studies holds considerable potential to more accurately understand the environment of animals and the drivers of their behavior.

Animal movement patterns can reflect how animals interact with their environment and which behaviors may have evolutionary and ecological implications for survival (Holyoak et al., 2008; Nathan et al., 2008), especially for highly arboreal animals that move through forests horizontally and vertically in their daily life. However, research on animal movement patterns in 3D environments has been hindered by the difficulty in constructing accurate 3D habitats. Innovative LiDAR technology can be used to acquire high-resolution (cm-level accuracy) 3D structure forest data (3DSF) in the field (Davies & Asner, 2014). LiDAR can provide detailed information on the structure of forest habitat, covering spatial scales ranging from less than 1 m^2 to over several hundred km^2. Integrating animal movement data with LiDAR-obtained 3DSF can greatly improve the accuracy of species habitat modeling, which is particularly useful for documenting the movement patterns of forest-dwellers, from individual trees to the entire home range.

Golden snub-nosed monkeys (*R. roxellana*) are the northernmost arboreal nonhuman primate species and are considered essential ecosystem engineers, promoting seed dispersal and regeneration of temperate forests (Chapman et al., 2013). However, mountainous temperate forests display high heterogeneity in structure and plant phenology, which can have substantial effects on animals, especially during winter when food is limited and temperatures are low (Hou et al., 2020). Golden snub-nosed monkeys spend most of their time (70% to 100%) in the canopy, engaging in diverse activities such as foraging, resting, sleeping, grooming, and breeding, including copulation and sexual solicitation. Although these monkeys move in groups, movement patterns vary among individuals within subgroups. Here, we integrated data on monkey movements obtained from ground surveys with 3DSF obtained from airborne LiDAR to characterize the effects of forest structure on the movement patterns and habitat use of golden snub-nosed monkeys in Guanyinshan National Nature Reserve (N33°35′–33°45′, E107°51′–108°01′) on the southern slopes of the Qinling Mountains in Shaanxi, China (Figure 1Aa). Specifically, we explored (1) whether the effects of forest structure environmental attributes on movement patterns differ among individuals and (2) whether monkey strategies related to food availability and thermal regulation influenced by 3DSF affect movement patterns.

The study focal band of free-ranging golden snub-nosed monkeys has been continuously studied since 2010 and is well habituated. During the study period, the band consisted of 95 individuals belonging to seven one-male units. The monkeys were categorized into five age-sex classes: adult males (>7 years old), adult females (>5 years old), subadult males (5–7 years old), subadult females (3–4 years old), and young (0–3 years old). We excluded the young class in this study given the difficulty in identifying sex. To track the movements of each focal monkey, GPS coordinates were recorded for each tree that the monkey moved to from the previous night's sleep site until it settled into the current night's sleep site (Figure 1Aa). Data collection was ceased for a day if the focal monkey could not be located. The final dataset

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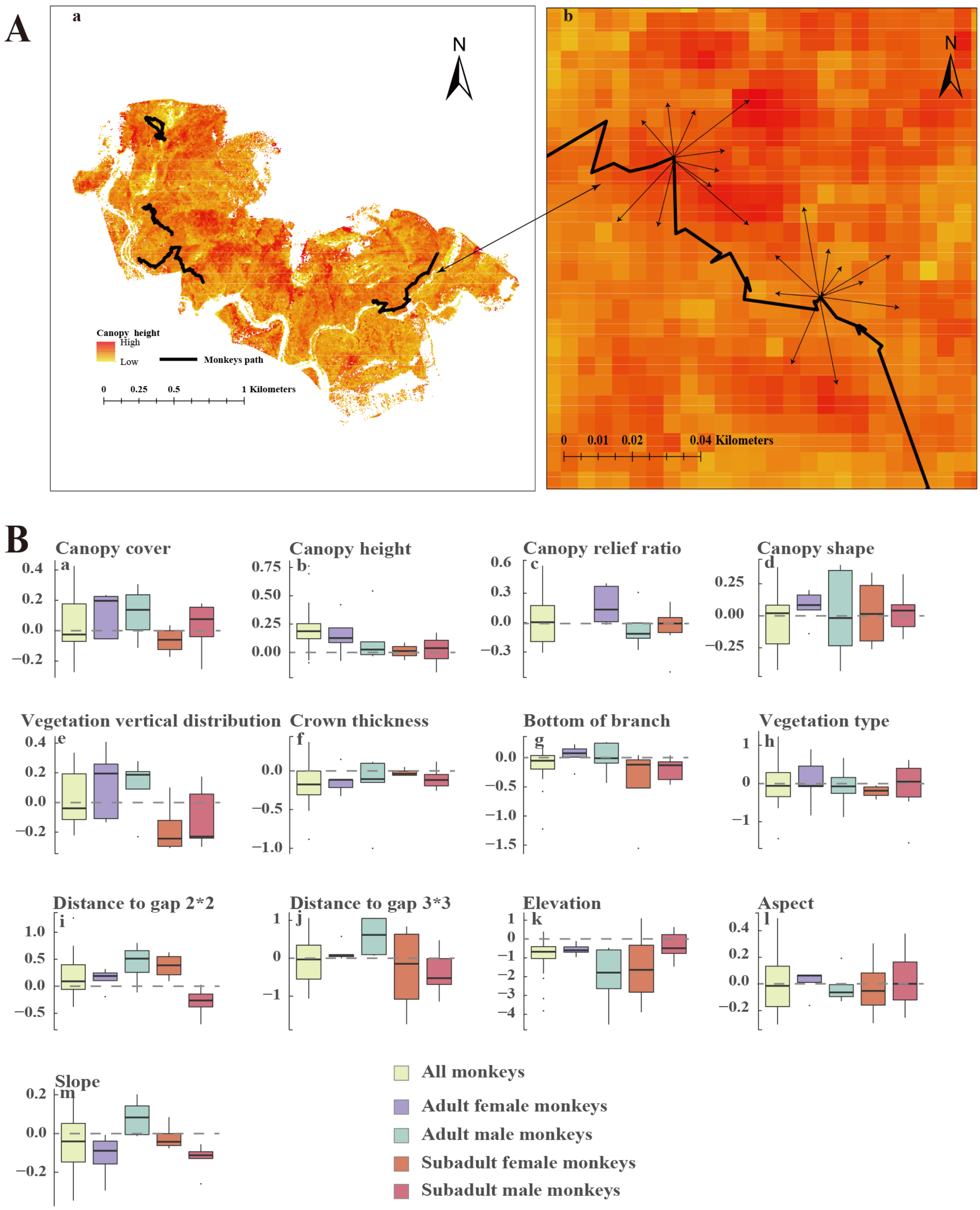
consisted of 51 day follows and 3 087 steps (i.e., linear paths between successive trees through which monkeys moved) of 20 individual monkeys, including 748 steps from five adult males, 741 steps from five adult females, 813 steps from six subadult males, and 785 steps from four subadult females (detailed information about field data collections is provided in Supplementary Materials). We used a RIEGL VUX-1UAV LiDAR scanner (Riegl, Austria) fixed on the unmanned aerial vehicle (UAV) to collect LiDAR data covering the whole area of monkey activity. Based on the LiDAR point cloud data, we carried out ground-filtering processing to separate ground and non-ground points. We then obtained a digital terrain model (DTM) and digital surface model (DSM) from the ground point clouds and vegetation point clouds, respectively, which were interpolated into raster grids with a spatial resolution of 0.5 m. A canopy height model (CHM) was then derived from the



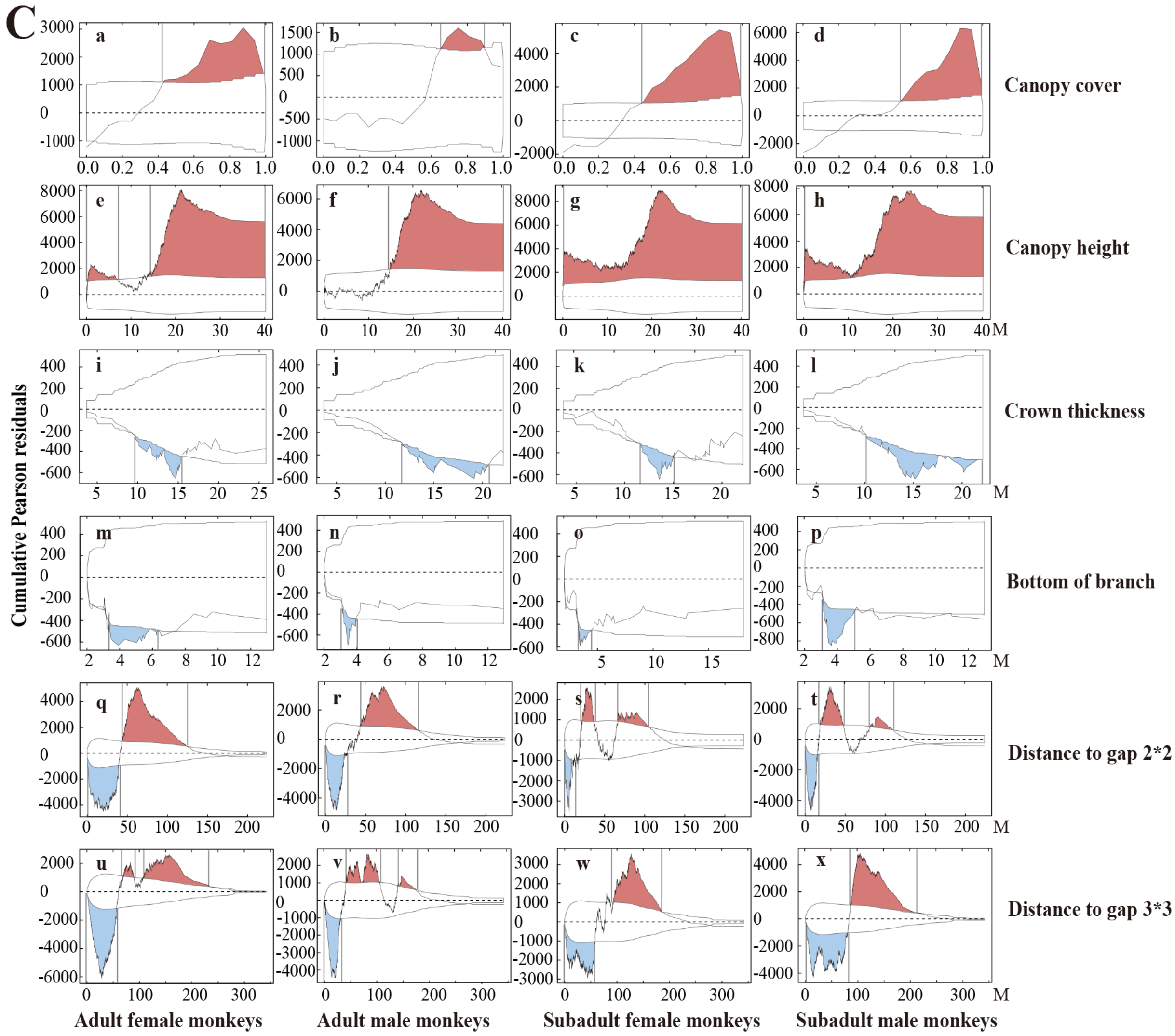


Figure 1 Study area and main results

A: (a) Canopy height within and around the study site, south of Guanyinshan National Nature Reserve, with monkey movement paths used in analysis. (b) Depiction of SSFs generated along an example movement path (black line is observed movement, gray lines are available steps monkey could have taken). B: Box plots of model-averaged coefficients from all monkeys and across monkey age and sex classes derived from individually applied SSFs. Solid line in each box indicates median for each age and sex class. Values above solid line at zero (positive coefficients) indicate selection for a given covariate, whereas values below (negative coefficients) indicate selection against a given covariate. C: Lurking variable plots against forest canopy cover (a–d), canopy height (e–h), crown thickness (i–l), bottom of branch (m–p), and distance to gap (2×2 m (q–t) and 3×3 m (u–x)) for influence on movement patterns in different monkey age and sex classes. Areas around the line at zero denote two standard-deviation error bounds. Black solid line indicates empirical curve of cumulative Pearson residuals. Residuals between solid lines with brown or blue indicate selection for or against a given scope of variables (above areas around the line at zero indicate significantly positive selection (brown); below areas around the line at zero indicate significantly negative selection (blue)).

difference between the DSM and DTM (Supplementary Table S1). Mean canopy height was measured from the CHM height within the 0.5 m grid and calculated in each pixel of a 2×2 m area. We calculated the canopy relief ratio, canopy shape, variability in vertical distribution of vegetation, crown thickness, and height of the bottom of the crown using the vertical distribution of LiDAR point cloud data (Supplementary Table S1) by LiDAR360 v5.0 (https://www.lidar360.com/archives/portfolio/lidar360). Tree species classification was based on individual tree detection from LiDAR-derived CHM segmentation. In the individual tree-based classification methods, point cloud data were used to derive neighborhood information on structural attributes, such as individual tree height, canopy size, and location, and the random forest was then used to discriminate vegetation types in the area (detailed information about 3DSF processing is provided in Supplementary Materials).

Qualitative analysis of the influence of spatially continuous variables was conducted using step selection functions (SSFs). SSFs are case-control functions used in resource selection functional analysis and are estimated from observed and random steps through conditional logistic regression (Davies et al., 2017). The probability of an individual monkey selecting a step was determined by comparing each observed step with a matched sample of 10 randomly drawn available steps. The SSFs were built using the *mclogit* package in R v3.6.1. A confusion matrix was used to evaluate model accuracy using the *caret* package in R v3.6.1. Kruskal-Wallis tests were conducted to compare differences in habitat selection among the four age and sex groups in R v3.6.1 (detailed information about qualitative analysis is provided in Supplementary Materials). Quantitative analysis was conducted using lurking variable plots (Liu et al., 2012) to assess the influence of spatially continuous variables on monkey movement patterns based on age and sex. This technique involves plotting cumulative Pearson residuals against continuous spatial covariates within a subregion to identify the systematic pattern that best accounts for specific spatial covariates. If the fitted model explains the continuous variables (null model), the cumulative Pearson residual values should be approximately zero. The null model overestimates or underestimates the effect of a variable on movement patterns when cumulative Pearson residual values exceed two times the standard deviation of the variable, indicating that monkeys either prefer or avoid areas in a particular variable range. All analyses were conducted in R v3.6.1 using the *maptools*, *raster*, *sp*, and *spatstat* packages (detailed information about quantitative analysis is provided in Supplementary Materials).

For golden snub-nosed monkeys, food availability and thermal regulation are key factors affecting survival and movement during the cold winter (Guo et al., 2018), consistent with the conceptual framework of movement ecology (Nathan et al., 2008). The 3D structure of forests is an external factor that affects the navigation and motion capacity of monkeys (Guo et al., 2008). Our SSF results revealed no significant differences in the use of upper canopy features, vertical complexity features, and substrate features by monkeys in the different age and sex groups (Figure 1Ba-m; Supplementary Tables S2–S4). However, integration of qualitative analysis from the SSF results (Figure 1Ba-m; Supplementary Tables S2–S4) and quantitative analysis from lurking variable plots (Figure 1Ca-x) revealed that the strength and direction of the responses to most habitat structure variables varied among monkeys in the different age and sex groups. Diversified use of habitat by golden snub-nosed monkeys can be particularly important when they experience both thermal and food stress (Figure 1Bc-h, 1Ci-p; Supplementary Tables S2–S4). The use of broadleaved trees during the winter not only facilitates maintenance of optimal body temperatures because such trees receive more solar radiation and heat than coniferous trees, but also provides the main food source for monkeys during winter (Supplementary Figure S1) (Hou et al., 2020).

Forest maturity, characterized by measuring canopy cover and height, was the main factor determining the movement patterns of golden snub-nosed monkeys (Figure 1Ba, b, Ca-h; Supplementary Tables S2–S4). Forest maturity likely enhances the lateral movement of monkeys across the canopy, as well as their ability to obtain food and avoid predators. Results showed that monkeys overall preferred areas with a canopy cover of 0.88 (Figure 1Ca, c, d) but adult males preferred areas with a canopy cover of 0.74 (Figure 1Cb). We suspect that adult males may prefer more open areas to better monitor the activities of family members and potential predators. Compared with adult females and subadults, adult males moved to slightly taller trees, which may facilitate the monitoring of family members, although body mass, predator avoidance, and mate-guarding strategies may also affect selection of specific canopy cover and height among the different age and sex groups (Figure 1Ba, b, Ca-h; Supplementary Table S2–S4).

High lateral connectivity within a forest minimizes the energetic costs of movement for arboreal primates. We found that adult monkeys were more sensitive to lateral connectivity changes in the forest than subadults (Figure 1Bi, j, Cq, r, u, v; Supplementary Tables S2–S4). Body mass was an important factor determining the crossing strategy of tree canopy gaps. Notably, adults preferred to descend to the ground or access lower canopy branches to traverse gaps, while subadults favored leaping (Figure 1Bi, j, Cs, t, w, x; Supplementary Tables S2–S4), which may minimize their exposure to terrestrial predators and represent an energy-conserving strategy compared to the more energy-costly behavior of adults.

The selection of environmental features, such as elevation, slope, and aspect, reflects the navigation capacity of monkeys, i.e., ability to orient themselves in space and select habitats to enhance fitness (Figure 1Bk, l, m; Supplementary Figure S2 and Tables S2–S4). These features are important determinants of resource distribution and microclimate, which substantially affect the distribution of wildlife. Generally, golden snub-nosed monkeys move at elevations between 1 400 and 3 300 m a.s.l. (Li et al., 2002; Yu et al., 2022). However, our study group tended to stay at lower elevations (1 300–1 650 m a.s.l.), especially during winter, likely indicating a trade-off between human disturbance and the availability of broadleaved tree food resources. Additionally, the monkeys exhibited a preference for slopes between 35°and 60°, which are less used by humans, and aspects between 180° and 260°, which are warmer than other areas and likely help maintain body temperatures during the cold winter months.

Golden snub-nosed monkeys reside in remote forested areas with rugged terrain. LiDAR is an effective technique for obtaining accurate habitat structure data and provides a robust alternative to field-based data. The collection of animal-related data and the acquisition of associated 3DSF and physiognomy by LiDAR are virtually simultaneous, reflecting the most natural use of the environment by animals, and thus producing more accurate results. Analysis of data on monkey movements and data at the landscape scale allowed us to quantitatively explore the threshold values of all variables selected by monkeys, thereby providing an intuitive understanding of the effects of habitat structure variables on monkey movement patterns.

Understanding the causes, patterns, mechanisms, and consequences of animal movement is critical for the conservation of functionally important species, as well as the management of degraded landscapes. A coherent framework for understanding animal movement should not only be conceptualized from the standpoint of animal movement itself but should also consider the impacts of the environment on movement. We integrated detailed visual observations of golden snub-nosed monkey movements with high-resolution airborne LiDAR data to clarify how habitat structure affects movement patterns and habitat use. Greater canopy cover and height increased the continuity of the movement paths of monkeys, likely enhancing their access to food and ability to thermoregulate and avoid predators. The high-resolution 3D forest structure data provided new insights into the differences in movement patterns of the different age and sex classes of monkeys. These differences may stem from sexual dimorphism and diverse social roles and ranks of individuals within the band. Considering the 3D environment will facilitate our understanding of the degree to which environmental factors influence behavior and fitness. Thus, we strongly advocate for the construction of 3D environments in ecological studies to more accurately depict the environment and drivers of animal behavior.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

The research presented in this paper adhered to the legal requirements of Guanyinshan National Nature Reserve, Shaanxi Province of China. In addition, all research followed the ethical protocols outlined by the International Primatological Society Principles for the ethical treatment of primates.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

B.G.L. and H.T.Y. conceived the ideas and designed the methodology. H.T.Y., S.L., W.T.S., R.H., Y.B.L., G.H., and X.W.W. collected the data. H.T.Y., S.L., W.T.S., and Y.W.F. analyzed the data. H.T.Y., R.H., C.A.C., Q.H.G., and S.L. wrote the manuscript. All authors read and approved the final version of the manuscript.

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