Research Square

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The nonlinear effects of forest cover and altitude on seasonal habitat selection of Asian elephants are related to temperature

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Abstract

Climate change threatens the survival of species, particularly large tropical mammals. Although some protection measures have been implemented, refined management is the key to ensuring their effectiveness. However, little is known about how large mammals adapt to climate change, especially thermal environment change, under complex circumstances, hindering efforts to develop specific policies. Here, we used a dataset from a continuous drone survey of Asian elephants on the southwestern border of China to illustrate seasonal differences in habitat use patterns, including forest, water, altitude, and the interaction between forest and altitude. We used resource selection function to examine the seasonal habitat selection of Asian elephant. We calculated the Johnson-Neyman intervals to identify management threshold, and clarify the relationship between temperature and forest ratio in habitats by fitting generalized linear mixed models. Overall, the interaction effect between the forest ratio and altitude varied with seasonal changes. Habitat with higher forest ratio is more likely to be utilized during wet season. Asian elephants use habitats with higher forest ratios in the wet season at high altitudes (above approximately 1,000 m) than those at low altitudes. Moreover, we found that temperature could explain seasonal patterns of habitat use. These findings suggest that large tropical mammals exhibit complex adaptive behaviors to thermal environment under different combinations of land types and topography. Our study highlights the importance of interactions between habitat features for seasonal adaptation and the need for fine-tuned management.

1 Introduction

Climate change is altering terrestrial ecosystems and threatening the survival of several species (Antão et al. 2022; Garcia et al. 2014). Although average climate conditions may deteriorate at a slow rate, climate change can lead to large climate fluctuations, increasing the risk of death to species (Garcia et al. 2014; Maxwell et al. 2019). Generally, animals can adapt to seasonal climate fluctuations through behavioral plasticity in range use to a certain extent, but this may be limited due to geographical barriers further amplified by human land modification (Elsen et al. 2020; Rowe et al. 2010). With climate change and human landscape expansion, understanding the adaptation behavior of animals under different conditions is crucial to adaptive conservation management.

Highly mobile species can potentially move to more suitable places in response to climate change-induced habitat threats. Many studies have shown that birds and small mammals can shift upslopes by adapting to increasing temperatures (Chen et al. 2011; Freeman et al. 2018; Rowe et al. 2010). Compared to smaller species, large mammals are disproportionately more affected by climate change because of their large size, requiring extensive habitats and slow life history traits (McCain and King, 2014). For mammals with large home ranges, adaptation through upslope shifts would shrink their available habitats because of the restrictions on mountain altitude, which may cause resources to decrease and further intensify the stress on the population. Thus, the effectiveness of shifting upslopes in mitigating the influence of climate change is limited. For forest-dwelling species, forests are important refuges, the buffering effects of which on the climate have been demonstrated. For example, as the

ambient temperature increased during the summer, moose (*Alces alces*) increasingly selected areas with denser canopy cover (Jennewein et al. 2020).

Seasonal activity of animals is a characteristic of their adaptation to cyclical changes in the environment (Varpe, 2017). Previous studies have found that habitat use by large mammals has certain seasonal characteristics owing to the seasonal availability of resources (Dupke et al. 2017; Lamichhane et al. 2018; Landry-Ducharme et al. 2024; Mulder et al. 2024). Considering that climate effects are increasing, seasonal habitat use patterns of large mammals may be influenced by climate change. A recent study on alpine chamois (*Rupicapra rupicapra*) has suggests that they can prevent the risk of extreme weather in summer and winter by adjusting habitat selection (Anderwald et al. 2024).

Most studies concerned the effect of food resources decline induced by climate change on animals. However, another important factor that limits animal survival, the thermal environment, has been neglected. Species that evolve in regions with low ambient temperature variation, such as the tropics, tend to be thermal specialists and have a relatively narrow thermal tolerance (Cadena et al. 2011; Ghalambor et al. 2006). Although warming-related local extinctions and range contraction appear to be more common in tropical mountain species than in temperate mountain species (Wiens, 2016), our understanding of how large tropical mammals adapt to climate change remains poor. A study recently showed that, in tropical forests, the understory near-ground temperature is 1.6°C lower than that in the open air, and the diurnal temperature range in the forest is on average 1.7°C lower than that in the open air (Ismaeel et al. 2024). Water could be effective sources to relieve heat stress (Mole et al. 2016; Martinez et al. 2024). Thus, understory and habitats with water sources are likely to be used more by animals to relieve heat stress in severe thermal environments.

Research on habitat use has mainly focused on land-cover types (Dickie et al. 2020), but land-cover type is not the only factor that determines habitat. Topography, such as altitude, is also an important factor influencing habitat. A previous study showed that favorable topography increases habitat suitability for golden eagle (*Aquila chrysaetos*) in temperate forests (Natsukawa et al. 2024). However, such studies are still lacking in terrestrial mammals. As altitude rises, air temperatures decrease, but thermal radiation received by terrestrial animals may increase. Considering that radiant heat exchange is more important than air temperature (Buckley and Huey, 2016; Mitchell et al. 2018), animals may have different habitats at different altitudes. Thus, the influence of the interaction between land cover and altitude needs to be clarified.

Asian elephants are large tropical mammals that face serious threats (Ripple et al. 2016). An adult Asian elephant needs at least 150 kg of food per day with a lot of water, and usually takes more than ten hours to feed (Vancuylenberg, 1977). Due to their few sweat glands, large size, and lack of evaporative heat-loss mechanism, heat dissipation in Asian elephants is inefficient when ambient temperatures exceed body temperature (Domínguez-Oliva et al. 2022; Weissenböck et al. 2012). Water is not only a basic necessity for life but can also be used to relieve heat stress. These characteristics render them more sensitive to environmental conditions. The shades under the canopy would be used by elephants when

the temperature is high (Kinahan et al. 2007; Mole et al. 2016). A recent study showed that they may expand their range in response to climate change (Bai et al. 2022). Elephants would use different habitat due to water and food limitation (Anoop et al. 2023; Lamichhane et al. 2018). However, little is known about how these species adapt to thermal environment variation by changing their habitat use on a large scale.

Here, we used a dataset from a nearly 3-year continuous drone survey of Asian elephants in Xishuangbanna, Yunnan Province, China, to address the following specific questions: (1) What role the interplay of among habitat features plays in determining seasonal habitat use patterns by elephants? (2) How are seasonal habitat use patterns influenced by climate? We hypothesized that (1) there is an altitude threshold for seasonal habitat use patterns because of different thermal conditions at different altitudes, and (2) seasonal temperature and precipitation changes could explain habitat use patterns because elephants are sensitive to heat.

2 Material and Methods

2.1 Study area

Xishuangbanna is located in Yunnan Province, China (21°10' – 22°40' N, 99°55' – 101°50' E) with the area of 19,096 km^2, and an altitude range of 477–2429 m (Figure S1). It is located on the northern edge of the tropics and has a subtropical rainforest monsoon climate that is warm and humid throughout the year, with dry (November to April) and wet (May to October) seasons. The average lowest and highest temperature in the coldest month (January) are around 13 ℃ and 26 ℃, those in the warmest month (July) are around 23 ℃ and 33 ℃. The mean precipitation is around 1,200–2,500 mm, and 85% of precipitation is in wet seasons. The terrain is mostly hilly and mountainous, with complex geological structures and a large undulating terrain. The vegetation type in this area is mainly evergreen forest. Its biodiversity is extremely high, with the largest wild Asian elephant population in China (Zhang et al. 2015).

2.2 Occurrence records

Occurrence point data of Asian elephants were obtained from remote sensing using an unmanned aerial vehicle dataset in Xishuangbanna (Yang et al. 2023). From March 2019 to December 2021, approximately 20 investigators used ten drones (DJI Matrice M300 RTK) with visual and infrared perception systems to track and detect the position of Asian elephants when the local early warning system detected that the Asian elephant was about to leave the forest in the reserve. The maximum flight time of the drones in a single flight can reach 43 minutes, covering 8 km^2 area. Although most positions were out of reserve, we believe this will not have a big impact on our analysis because Asian elephants are considered to be specialists of the forest edge, preferring a combination of natural forest and secondary vegetation, and do not always prefer protected areas with undisturbed vegetation (de la Torre et al. 2021, 2022), so potential sampling bias may be slight. Because individual elephants could not

be reliably identified from drone imagery, it was not possible to assign. Accordingly, our analysis focuses on population-level habitat use patterns.

2.3 Climate variables

Average monthly temperature and precipitation data from 2019 to 2020 (at a 1 km resolution in China) were obtained from the National Tibetan Plateau Data Center (https://data.tpdc.ac.cn/home). These datasets were spatially downscaled from the 30' Climatic Research Unit time series datasets with the climatology datasets of WorldClim using delta spatial downscaling, and further were verified by 496 independent meteorological observation points were used for verification (Peng et al. 2019).

2.4 Habitat variables

Land cover data were obtained from the 30 m annual China Land Cover Dataset (Yang and Huang, 2021). Considering the duration of the survey, we used data only from 2020 because the land cover did not change significantly in survey years. We rescaled the dataset to a 1 km grid and calculated the forest ratio and distance to water in each grid. Altitude data were obtained from a dataset of a 1 km resolution digital elevation model in China published by the National Cryosphere Desert Data Center (http://www.ncdc.ac.cn). Notably, most land types of Asian elephants are forest and farmland (farmland ratio could be approximately one minus the forest ratio), and we mainly focused on the combined effect of land cover and topography. Thus, we used only forest ratio (FR), distance to water (DW), and altitude (ALT) to illustrate habitats in the following analysis. We chose these variables because they were important to help animals to adapting to thermal environment (Table 1).

Table 1
Environment variables used in this study and their potential influence.

Variables	Unit	Potential influence	Sources
Average monthly temperature (TMP)	0.1°C	indicate macro climate condition and thermal environment	Peng et al. 2019
Average monthly precipitation (PRE)	mm	indicate macro climate condition, could relieve heat stress	Peng et al. 2019
Forest ratio (FR)	-	shades formed by canopy could relieve heat stress (Ismaeel et al. 2024; Kinahan et al. 2007; Mole et al. 2016)	Yang and Huang, 2021
Distance to water (DW)	m	water sources, could relieve heat stress via spraying water over the body (Mole et al. 2016; Martinez et al. 2024)	Yang and Huang, 2021
Altitude (ALT)	m	The higher the altitude, the lower the temperature, but the solar radiation may increase, and cause heat stress (Buckley et al. 2013; Scherrer and Körner, 2010)	National Cryosphere Desert Data Center (www.ncdc.ac.cn)

2.5 Statistical analysis

When using drones for positioning at high altitudes, the recorded locations may deviate from the actual positions of the animals. Therefore, our goal was to determine the patterns of habitat use by Asian elephants on a medium scale. Considering the spatial resolutions of environment variables used, we selected 1 km as the minimum spatial unit for this study, which was also widely used in species distribution modelling on a medium scale (KramerSchadt et al. 2013). Since there was no standardized sampling time interval for the occurrence data, we divided the study time period into multiple continuous fixed time windows (7-day, 15-day, 30-day, 45-day, 60-day), and spared the data to only one data point within a 1-km^2 grid in each time window to avoid bias caused by the sampling frequency. Due to the results are similar in windows of different time lengths (Figure S2), we only reported the results of 30-day window.

We used the resource selection function (RSF) to identify the habitat selection pattern of Asian elephants between seasons. Specifically, after ensuring that there are no strongly correlated habitat variables (Table S1), we used Z-score method to standardize habitat variables (forest ratio, altitude, and distance to water) to fit a model (Table S2; Model 1) with the “year” as a random effect. In addition to single terms of habitat variables, we also added the interaction terms between forest ratio and altitude, as well as interactions between season and other terms to address our first question. We fitted the model using 50 available points per used point and checked the converge (Figure S3). We checked the final model for multicollinearity by calculating the variance inflation factor (VIF) (Table S3).

We used the logistic regression to identify differences between habitats where the elephants have been used in wet seasons versus dry seasons. First, we created a seasonal balance subset (n = 3148) from the refined occurrence data and encoded the wet season as 1 and the dry season as 0, because this modelling framework is only valid if it is assumed that the two groups are equally available (Northrup et al., 2022). We used generalized linear mixed models (GLMM) (binomial family, logit link) to evaluate the difference between seasons (Table S4; Model 2), and checked for multicollinearity (Table S5). Third, we randomly selected background points of the same sample size in the region of Xishuangbanna and mixed them with the dataset from the first step, constructing the variable "occur" which is a binary variable that indicate presence vs available points. We added “occur” and its interactions with other terms to the model, and calculated 95% confidence intervals for each term using the bootstrap method to confirm that the patterns identified by our model were not due to geospatial sampling (Table S6; Model 3). If the interactions between “occur” and other variables were significant, it indicated that the presence or absence of elephants influenced the observed seasonal differences in habitat variables. Therefore, the seasonal habitat differences of habitat detected by the first model can be attributed to elephant.

To explore the interaction between forest ratio and altitude and identify the threshold (Hypothesis 1), we calculated Johnson-Neyman intervals of Model 2. It provides a clear threshold range that explains when the effect of the predictor variable is significant or insignificant, and is extremely effective in exploring the interaction between moderators and predictors (Johnson and Fay, 1950; McCabe et al. 2018). We

made slight changes to package “interactions” (Long, 2024) to use it calculating Johnson-Neyman intervals on Model 2 with altitude as the moderating variable (see Supplementary Information Text S1).

Subsequently, we examined how climate correlated with forest ratio to test our second hypothesis. Due to the strong correlations between temperature and precipitation, only temperature was used as a climate variable for subsequent analysis. The forest ratio is in a closed interval from 0 to 1, and traditional models have errors in estimation. The ordered beta regression can be estimated with or without observations at the bounds, and as such is a general solution for proportional data. It is also more efficient than other solutions while fully capturing nuances in the outcome. We fitted an ordered beta regression with forest ratio as the response variable (Kubinec, 2023), other variables (altitude, distance to water, temperature), and their interactions as explanatory variables by using the package “glmmTMB” (Brooks et al. 2017). Finally, we constructed full models (Tables S7), selected the most suitable model based on AICc (Model 4; Table S8), checked for multicollinearity (Table S9), and calculated the Johnson-Neyman intervals to assess the interaction effect.

All data preparation and analysis were performed in R 4.4.2 and ArcGIS Pro 2.8.0.

3 Results

3.1 The habitat selection patterns between seasons

The resource selection function (Model 1; Table S2) indicated that the forest ratio were negative to predict the habitat used by elephants (FR 95% CI: [-0.42, -0.34]; Fig. 1, Table S2). The altitude and distance to water were significantly negative as well (ALT 95% CI: [-0.28, -0.16], DW: [-0.30, -0.17]; Fig. 1, Table S2). Habitat nearer water would be more used in wet seasons than in dry seasons (Seasons × DW 95% CI: [-0.26, -0.07]; Fig. 1, Table S2). Higher-altitude habitat would be more used in wet seasons than in dry seasons (Seasons × ALT 95% CI: [0.02, 0.17]; Fig. 1, Table S2). We also found that the interaction effect between the forest ratio and altitude varied with seasonal changes (Seasons × FR × ALT; Fig. 1).

3.2 Seasonal differences of used habitat

Our model (Model 2; Table S4) showed that habitat with higher forest ratio is more likely to be utilized during wet season (95% CI: [0.05, 0.22]; Fig. 2A, Table S4). No significant effect of altitude was observed (95% CI: [− 0.12, 0.03]; Fig. 2A, Table S4). However, there was an interaction between the forest ratio and altitude (95% CI: [0.10, 0.24]; Fig. 2A, Table S4). The distance to water was significantly negative (95% CI: [− 0.11, − 0.25]; Fig. 2A, Table S4). Moreover, we detected an interaction between habitat-use and some habitat variables (Model 3; DW, FR × ALT; Fig. 2B, Table S6), which illustrated that the different patterns shown by the model can be attributed to the Asian elephant and not the illusion caused by spatial sampling.

At high altitudes, higher forest ratio in the habitat was observed in wet seasons, whereas a lower forest ratio in the habitat was observed in dry seasons (Fig. 3A). In contrast, the probability of being observed

during the wet season increased with the forest ratio of the habitat (Fig. 3A). The forest ratio coefficient increased from negative to positive with increasing altitude (Fig. 3B). There were two altitude thresholds for the significance of the forest ratio of the habitat in predicting the occurrence season. Between 714 m and 959 m, the forest ratio was not a significant variable for predicting the seasons (Fig. 3B).

3.3 Used habitats are correlated to temperature

Ordered beta regression (Model 4; Table S8) showed that there were positive relationships between temperature and forest ratio at high altitudes, but these relationships became negative with decreasing altitude (Fig. 4). Between 1084 m and 1229 m, temperature was not a significant predictor of the forest ratio (Fig. 4B).

4 Discussion

Our findings demonstrate the complex combination of the effects of land cover and topography on the use of habitats by elephants. Furthermore, during the wet season, habitats with a higher proportion of forest were used at higher altitudes (above approximately 1,000 m) compared to lower altitudes. No significant differences were observed in the forest habitat ratio at low altitudes between seasons. In addition, these patterns could be partly explained by temperature, but not by precipitation.

4.1 The habitat selection patterns between seasons

Our results showed that elephants were far from water in the dry season, but near water in the wet season, which was contrary to some other studies (Anoop et al. 2023; Chui et al. 2024). In our research area, the vegetation type is mainly evergreen forest which is different from those studies. Water content in food can satisfy the water requirement, and there could be tiny streams that are adequate for elephant needs; therefore, it is not necessary to consume a large amount of water through water sources in the dry season. However, during wet seasons, elephants will have an increased need for water to relieve thermal stress, and tiny streams will struggle to meet their heat dissipation needs. Large areas of water can help animals cool their body temperature, further relieving heat stress (Mole et al. 2016; Martinez et al. 2024).

We found that Asian elephant responded differently to different combinations of forest ratio and altitude in different seasons. Food and heat balance are essential conditions for animals to survive. Food is generally not lacking during the wet season, but high thermal stress during the wet season may pose a threat to Asian elephants because of the increasing solar radiant at higher altitude (Domínguez-Oliva et al. 2022; Rozen-Rechels et al. 2020). Forest canopies can relieve high temperatures and solar radiant (Mole et al. 2016). Thus, Asian elephant would use habitat with higher forest ratio at high altitude during wet seasons.

4.2 Seasonal differences of used habitat

We also found that the interaction between the forest ratio and altitude plays a role in predicting seasonal variations in used habitat. The impact of forests on animals mainly involves directly providing resources such as food and water, as well as places to shelter from natural enemies and human disturbance (Wade et al. 2013). However, altitude mainly affects animals indirectly through environmental conditions, such as soil and climate (Chibeya et al. 2021; Hof et al. 2012). Most animals take advantage of habitats with different resources, depending on the environmental conditions (Magioli et al. 2023; William et al. 2018). Thus, the interaction effects of forest ratio with altitude were formed, and it was unreliable to use only the simple effects of land cover and topography to describe habitat use.

Consistent with our expectations (Hypothesis 1), we found clearer seasonal change patterns in forest ratios above around altitude 1,000 m than at all altitudes. Asian elephants would increase the use of forests in wet seasons and increase the use of croplands in dry seasons. At high altitudes in tropical montane forest, although the air temperature was lower, exposure of animals and the ground to solar radiation was enhanced (Buckley et al. 2013; Scherrer and Körner, 2010). Environmental heat exchange is not governed primarily by air temperature (Buckley and Huey, 2016). For most large mammals in hot natural habitat, the radiant heat exchange is more important than air temperature (Mitchell et al. 2018). The increase solar radiation may have resulted in more heat being absorbed by the animals than in the plains, further causing heat stress. Therefore, a habitat with a high forest ratio would be the most suitable for elephants during high-temperature wet seasons at high altitudes. In dry seasons, heat radiation is no longer a threat because of the reduction in solar radiation and drop in temperature. Food shortages due to water scarcity have become a crucial factor limiting elephant activities. Human-managed cropland provides a steady stream of food that matches the needs of elephants.

4.3 Used habitats are correlated to temperature

Partially in line with our expectations (Hypothesis 2), seasonal temperature differences may explain the habitat use of elephant. In this study, we found that the interaction between temperature and altitude had a significant effect on the forest ratio of habitat used by Asian elephants. Temperature was positively correlated with the proportion of forest cover in habitats used by elephants at higher altitude, which was negative at lower altitude. Generally, climate affects animal habitat uses in two main ways. First, the climate directly makes the habitat more hostile, exceeding the physiological tolerance limits of animals (Antão et al. 2022). Animals can adapt to these changes through behavior, such as shifting to other places and increasing the use of specific resources. Second, the climate reduces the availability of resources, such as food and water, further intensifying the threat to animals (Kuletz et al. 2024; Penteriani et al. 2019). The animals were then moved to other places to find available resources. Thus formed the positive relationship between temperature and forest cover in habitats. However, due to we were not comparing used habitat against available habitat in modeling the effect of climate on forest ratio in habitats selected, the positive relationship may not imply the causal effect that rising temperature cause an increase in the proportion of forests used by elephants at high altitude. Thus, more evidence is needed to prove the climate effect on habitat selection of elephants. Food resources

are also important factors affecting habitat use by animals (Cain et al. 2017; McClelland et al. 2020), the lack of food-related variables may make our results unrobust in different food resource level.

4.4 Implication for conservation

Majority of the current research on conservation is based on a set of simple assumptions, ignoring the complex interactions between organisms and the environment and the variability of such interactions. As a result, management measures derived from the theories in these studies are often not spatially or temporally variable. These theoretical limitations in the studies may be one of the reasons why it is currently difficult to implement refined management on a large scale. We illustrated the feasibility and necessity of incorporating complex interactions into conservation theory, which is consistent with a recent study (Natsukawa et al. 2024).

Most current measures for large mammal conservation are simple or crude, probably because of cost constraints. Large mammals tend to have larger ranges, indicating that the area to be managed is larger. Single management measures such as area closures and grazing and logging bans can be simple, effective, and less costly to enforce (Pekor et al. 2019). However, these management measures ignore the complexity and dynamics of ecosystems, particularly in areas with diverse environmental conditions. This may result in reduced conservation effectiveness and increased unit costs (Vigo et al. 2024).

Our study further provides a brief case demonstrating how the interaction between land cover and topography can be incorporated into a policy making framework. We identify the altitude threshold of habitat use of Asian elephant adapting to temperature changes by calculating the Johnson-Neyman intervals, and suggest that local conservation management of Asian elephants needs to be differentiated at an altitude of about 1,000 m. At low altitude, focusing on food sources to meet the food needs of Asian elephants. At high altitudes (above approximately 1,000 m), maintaining the integrity of forest habitats forest habitats and increasing water sources. These managements may mitigate human-elephant conflict while achieving conservation of Asian elephants.

5 Conclusion

Our research reveals the complexity of animal habitat uses and demonstrates the importance of incorporating interactions between land type and topography, thus providing new insights into the mechanisms of the formation of seasonal habitat use patterns. Meanwhile, we examined the relationship between seasonal elephant habitat-use and environmental features that are potentially related to thermal stress. Given the intensification of climate change and the expansion of tropical human landscapes, improving our understanding of animal responses in complex environments and more precise management could help reduce threats to large tropical mammals.

Abbreviations

FR

forest ratio
DW
distance to water
ALT
altitude
RSF
resource selection function

Declarations

Data accessibility statement

The dataset supporting the conclusions of this article is available in the Zendo Digital Repository, https://doi.org/10.5281/zenodo.15173265.

Author contributions:

L. L. and L. Z. conceived the study. Z. C. collected and analyzed the data. L. L. and L. Z. supervised the research. L. Z. was involved in acquiring funding for the study. Z.C. wrote the initial draft of the manuscript with input from L. L. and L. Z. All authors provided comments and edits and gave final approval for publication.

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Declaration of Competing Interests

The authors declare no conflict of interest.

Ethics, Consent to Participate and Consent to Publish declarations:

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Figures

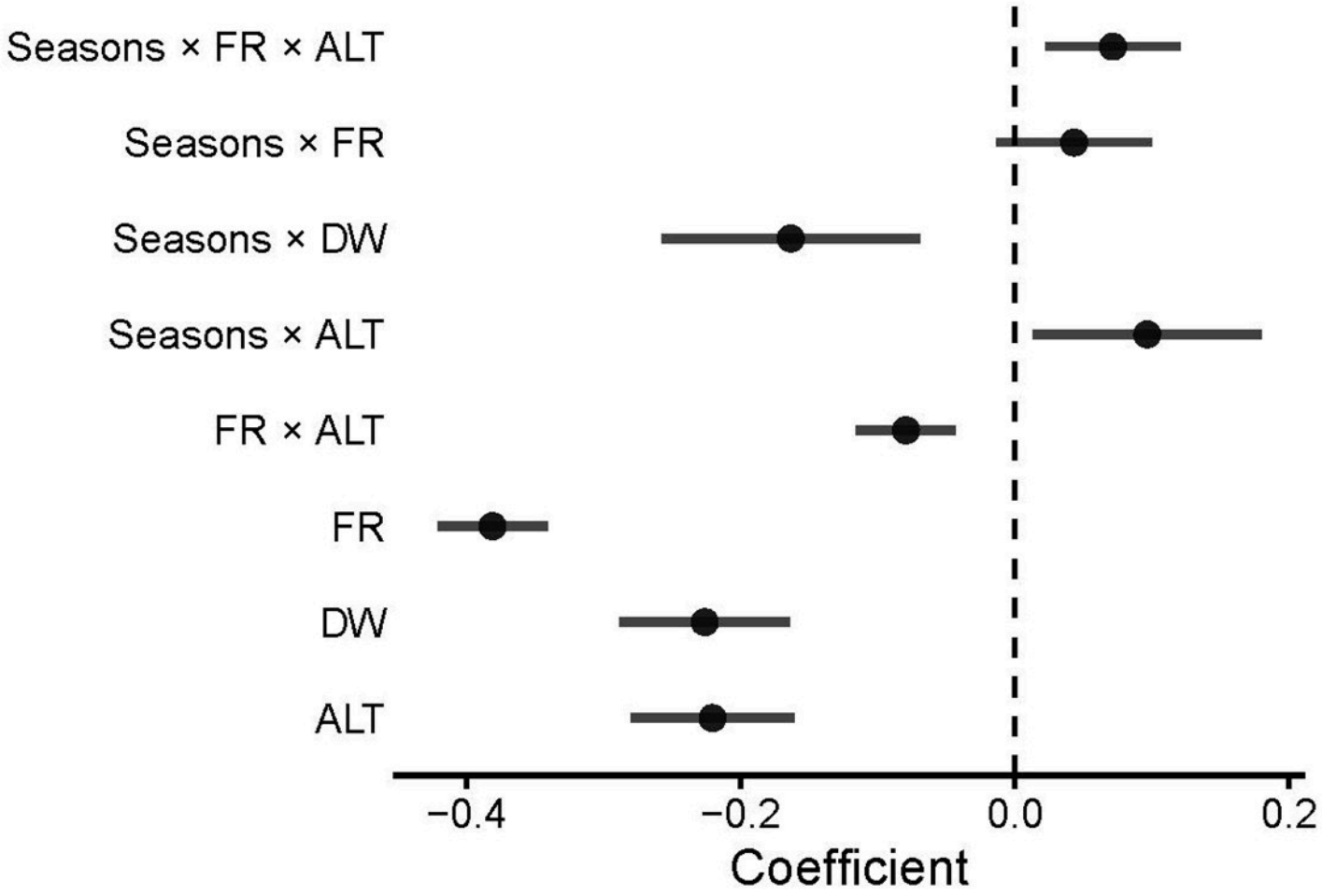


Figure 1

Habitat selection patterns estimated by resource selection function (mean ± 95% CI). FR, forest ratio; DW, distance to water; ALT, altitude.

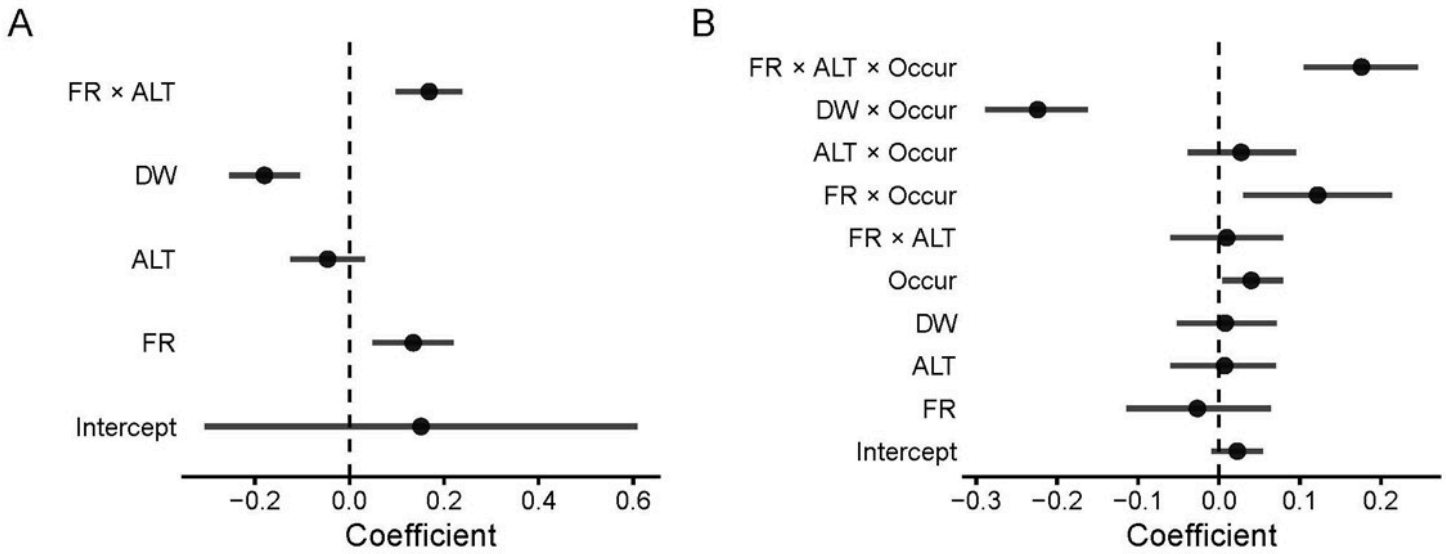


Figure 2

The seasonal habitat using patterns of Asian elephants is shown by generalized linear mixed models (GLMMs). (A) The coefficient (mean ± 95% CI) of GLMM on occurrence dataset (n = 3148). (B) The bootstrap coefficient (mean ± 95% CI) of GLMM on the mixed dataset (n = 6296). FR, forest ratio; DW, distance to water; ALT, altitude.

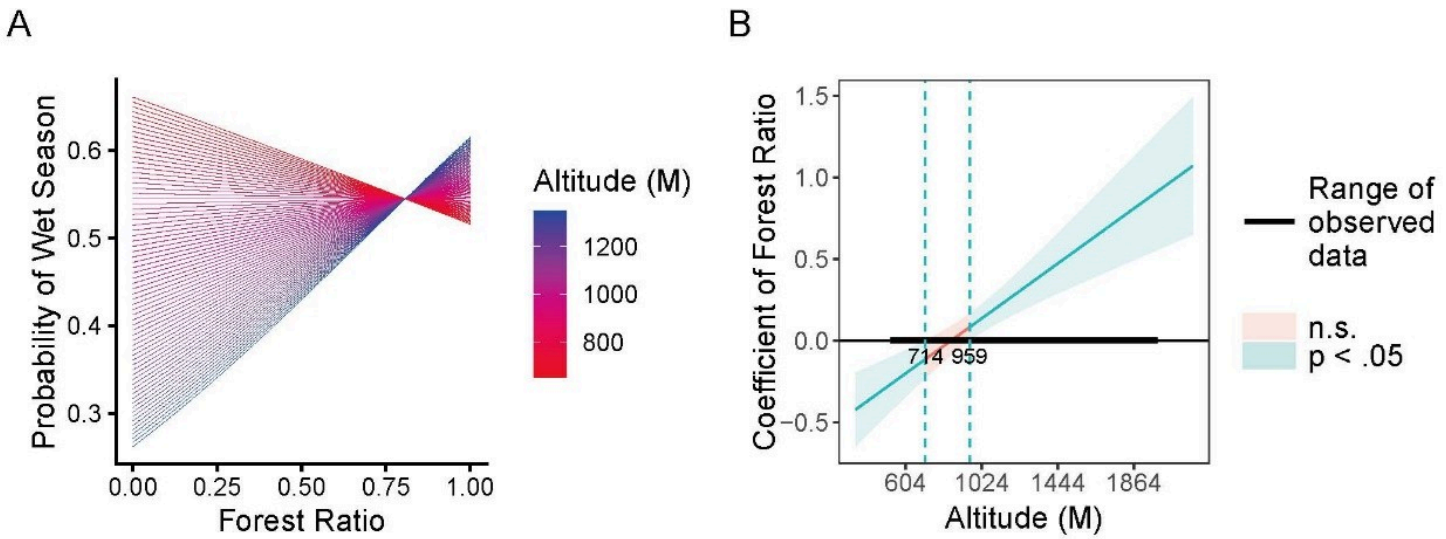


Figure 3

The interaction of forest ratio and altitude. (A) Predictions of occurrence season by forest ratio at different altitudes. (B) The Johnson-Neyman intervals of altitude moderating forest ratio's effect. Vertical dashed lines were threshold of significant. Shaded areas showed 95% confidence interval.

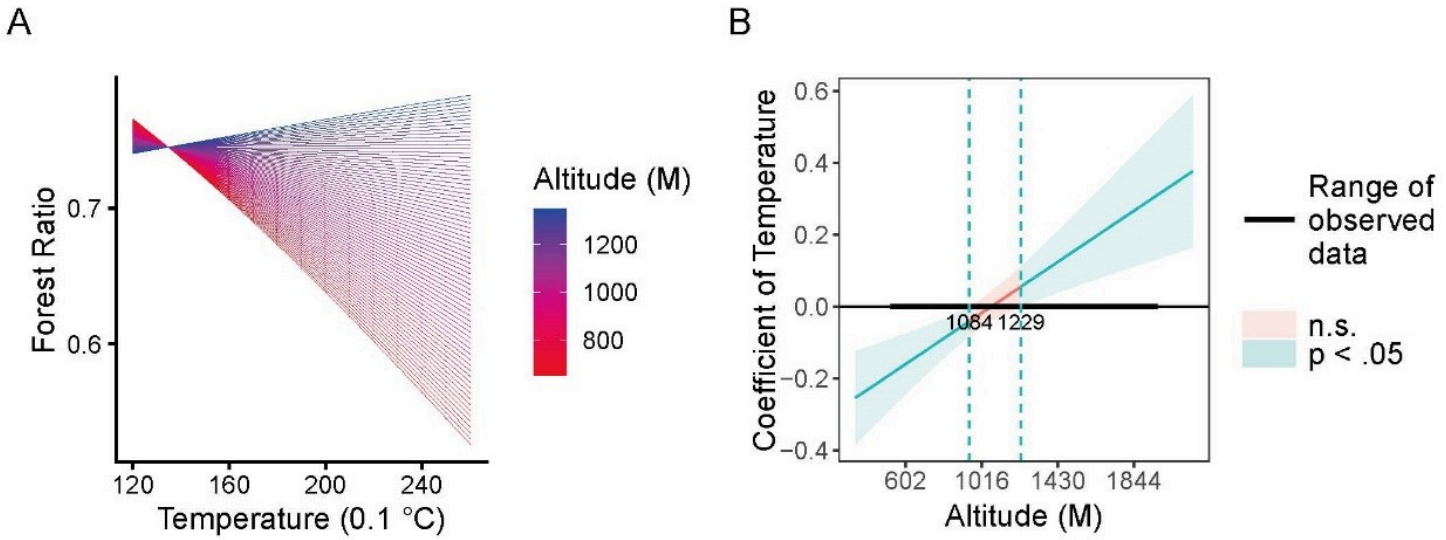


Figure 4

The interaction of temperature and altitude. (A) Predictions of forest ratio by temperature at different altitudes. (B) The Johnson-Neyman intervals of altitude moderating temperature's effect. Vertical dashed lines were threshold of significant. Shaded areas showed 95% confidence interval.

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