



## MODELLING THE DISTRIBUTION OF THE PROBOSCIS MONKEY (*NASALIS LARVATUS*) IN SABAH (BORNEO) BASED ON REMOTELY SENSED HIGH-RESOLUTION GLOBAL CLOUD DYNAMICS

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### Abstract

Proboscis monkeys, *Nasalis larvatus* (Wurmb, 1787), are indigenous to the island of Borneo and are considered one of its most emblematic species. Today the conservation status of this primate is classified as Endangered on the IUCN Red List and listed under Appendix I of CITES, prohibiting all international commercial trade. In the Malaysian state of Sabah, the species is listed as totally protected and cannot be hunted. Continuing studies suggest that the number of proboscis monkeys has been decreasing in recent years. These studies have identified various factors contributing to this decline and its potential consequences. In order to carry out a thorough assessment of the conservation status of the species it is essential to have a good understanding of the animal's ecology and habitat requirements and to use research-based approaches. One of such are species distribution models (SDMs), which in recent decades have become widely used tools in ecology by relating species occurrences to environmental data to gain ecological insights. In this work, we specifically evaluated the effect of environmental parameters such as cloud cover to predict the potential distribution of the proboscis monkey in Sabah. Cloud cover, a seemingly simple atmospheric phenomenon, exerts a profound influence on a wide range of ecological biological processes, yet the assessment of its importance has remained remarkably limited. For modelling purposes the 'flexsdm' R (v. 3.3.3) modelling package was employed for testing out the Maximum entropy (Maxent) algorithm, one of the most widely used SDM modelling methods. Model evaluation gave satisfactory results and the resulting model found a high level of suitability for proboscis monkeys in nearshore areas. A concerning discovery is that perhaps less than 13% of Sabah's area is suitable habitat for proboscis monkeys, raising questions about their long-term viability. Cloud cover, particularly average annual cloudiness, is a key environmental factor influencing the distribution of proboscis monkeys in Sabah. The conversion of Borneo's forests to oil palm plantations can negatively impact cloud properties, potentially threatening the monkeys' habitat.

### Cite as

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## Моделювання поширення носача (*Nasalis larvatus*) в штаті Сабах (Борнео) на основі дистанційного зондування глобальної динаміки хмарного покриву

Володимир Титар, Ірина Козиненко, Михайло Навакатикян

**Резюме.** Носач, *Nasalis larvatus* (Wurmb, 1787), є ендеміком острова Борнео, і його вважають одним із найбільш його символічних видів. Сьогодні природоохоронний статус цього примата визначений як «Зникаючий» у Червоному списку МСОП і внесений до Додатку I CITES, що забороняє будь-якої міжнародної комерційної торгівлі цим видом. У малайзійському штаті Сабах вид занесений до списку видів, які повністю охороняються та на яких заборонено полювання. Триваючі дослідження свідчать про те, що кількість цих мавп в останні роки скорочується. Ці дослідження виявили різні чинники, що сприяють цьому, і якими можуть бути його потенційні наслідки. Щоб провести ретельну оцінку природоохоронного статусу виду, важливо добре розуміти його екологію та вимоги до середовища існування, та використовувати підходи, які засновані на наукових розробках. Одним з таких підходів є моделювання просторового розподілу видів (SDM), яке в останні десятиліття стало широко вживаним інструментом в екології, пов'язуючи географічні локалітети видів із даними про навколишнє середовище, щоб отримати таким чином екологічну інформацію. У цій роботі ми спеціально вивчали вплив параметрів середовища, таких як хмарний покрив, щоб передбачити потенційне поширення носачів в Сабаху. Хмарний покрив, здавалося б, просте атмосферне явище, справляє глибокий вплив на широкий спектр екологічних та біологічних процесів, але оцінка його важливості залишається надзвичайно обмеженою. Для цілей моделювання використовувався пакет «flexsdm» R (версія 3.3.3) та був протестований алгоритм максимальної ентропії (Maxent), одного з найбільш популярних методів моделювання SDM. Оцінка моделі дала задовільні результати, і отримана модель виявила високий рівень придатності середовища для мавп у прибережних районах. Тривожне відкриття полягає в тому, що можливо менше 13% площі Сабаха придатні для проживання цих мавп, що викликає сумніви щодо їхнього довгострокового виживання. Хмарний покрив, особливо середньорічна хмарність, є ключовим екологічним фактором, що впливає на поширення носачів у Сабаху. Перетворення лісів Борнео на плантації олійної пальми може негативно вплинути на властивості хмар, потенційно загрожуючи середовищу існування мавп.

**Ключові слова:** носач, Сабах, моделювання поширення, Максент, динаміка хмарного покриву.

### Introduction

Endemic to the island of Borneo, proboscis monkeys, *Nasalis larvatus* (Wurmb, 1787), are large and sexually dimorphic primates from the subfamily Colobinae [Bennett & Gombek 1993], representing one of the island's iconic and unique species. Proboscis monkeys are well distinguished from other primates for their large, red, and protruding noses [Bennett & Gombek 1993]. These monkeys are known to be the largest representatives of colobines and they are the only members of the genus *Nasalis* [Napier & Napier 1967; Medway 1977]. They are largely restricted to coastal lowland mangrove, riparian, and swamp forests [Kawabe & Mano 1972; Wolfheim 1983; Salter *et al.* 1985; Boonratana 1993; Bernard 1997] up to 750 km inland, but usually less than 55 km from the coast, and at altitudes below 350 m above sea level [Medway 1977; Salter & Mackenzie 1985; Bennett & Sebastian 1988; Meijaard & Nijman 2000]. Proboscis monkeys are closely associated with water-ways, traveling inland to forage (generally up to 1 km) and returning to their sleeping sites along the river edge every evening [Bennett & Sebastian 1988; Yeager 1989; Boonratana 2000].

Today the conservation status of this primate is classified as Endangered on the IUCN Red List [Meijaard *et al.* 2008] and listed under Appendix I of CITES<sup>1</sup>. In Sabah, the species is listed as totally protected. Hunting, degradation of their habitats by logging and conversion into agricultural land (particularly for palm oil production), were identified as the major factors in the decline of their population [Meijaard & Nijman 2000].

<sup>1</sup> Website: CITES. Appendices I, II and III, valid from 25 May 2024 <https://cites.org/eng/app/appendices.php>

There are indications that proboscis populations have been declining over the past decades [e.g. Chapman & Peres 2001; Fuller *et al.* 2004] and subsequent research has reinforced the trend, often delving deeper into the specific causes and impacts [Toulec *et al.* 2020; Atmoko & Mukhlisi 2021].

Unfortunately, the lack of updated information on the current situation, including even distribution, hampers attempts to carry out a thorough assessment of the conservation status of the species. In this respect, it is essential to have a good understanding of the animal's ecology and habitat requirements and to use research-based approaches. Amongst such are species distribution models (SDMs), which have become in recent years one of the most widely used tools in ecology [e.g. see Guisan & Zimmermann 2000; Guisan & Thuiller 2005]. The principle of SDMs is to relate species occurrences to environmental data in order to gain ecological insights [Elith & Leathwick 2009]. This family of methods has a broad range of applications, including the identification of areas for conservation and guiding the efforts to locate new populations of known species of conservation concern [Fois *et al.* 2018]. The resulting habitat maps, which range from zero to one, show areas where the species is predicted to reside. This information is crucial for conservation efforts and selecting suitable reserve locations.

In this respect, a recent innovative study has aimed to analyse the habitat suitability of the proboscis monkey on Borneo using a multi-machine-learning approach [Sakti *et al.* 2024]. This study integrated physical, vegetational, meteorological, and human activity data to develop a comprehensive SDM and identified a high level of habitat suitability for proboscis monkey in nearshore areas. The results of this research provide valuable insights for the formulation of well-planned development programs for proboscis monkeys and will contribute to the accurate identification of potential habitats, thereby providing support for conservation efforts aimed at safeguarding this endangered species. In our work, we specifically evaluated the effect of environmental parameters such as cloud cover to predict the potential distribution of species in Sabah. This is because cloud cover can influence numerous important ecological processes, including reproduction, growth, survival, and behaviour, yet the assessment of its importance has remained remarkably limited [Wilson & Jetz 2016; Pacayán *et al.* 2019; Gerstner *et al.* 2024].

## Material and Methods

### *Study area*

The Malaysian state of Sabah (76 000 km<sup>2</sup>) is situated between latitudes 4°8' and 7°22' north of the equator on the north-eastern tip of Borneo. The western and eastern regions are divided by the Crocker Range, which runs almost parallel to the west coast, extending from the southern end of Marudu Bay in the north and southwards along the western part of the state to the Sarawak border. The narrow western lowland plains contain areas of low, flat ground that is densely populated, while eastern Sabah is characterised by low dissected hills, gentle slopes and poorly drained flatland and low-lying swampy zones that have been extensively logged and converted to permanent agriculture where soil and terrain is suitable [Payne 1988].

In Sabah, populations of proboscis monkeys are known to exist mainly in the freshwater wetlands around Dewurst Bay, along the Kinabatangan, Segama, and Sugut rivers in the eastern deltas and in the Klias Peninsula on the west coast [Davies & Payne 1982].

### *Species presence records*

For creating SDMs, generally geographic coordinates (longitude and latitude) of record localities of the species were used. The occurrence data were collected from GBIF [GBIF.org 2024] supplemented by our own observations in the Klias Peninsula (Fig. 1) and Labuk Bay made in 2020. The record localities were compiled into a CSV database (.csv).

A total of 985 records of the proboscis monkey in Sabah were obtained. We cleaned occurrences as recommended in the literature of data cleaning [Chapman 2005] and duplicate records removed using the corresponding module in SAGA GIS, resulting in 565 observations dating from 2000.

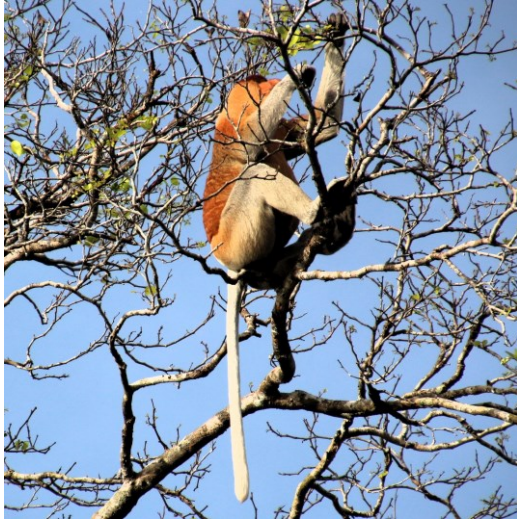


Fig. 1. Proboscis monkey (male) nearby to the Padas Damit Forest Reserve next to the Kliias River, 6 January 2020, photo by M. Navakatikyan.

Рис. 1. Носач (самец) в околицях лісового заповідника Падас Даміт поряд з рікою Кліас, 6 січня 2020 р., фотограф М. Навакатикян.

### ***Environmental data***

We included the MODIS-derived mean annual cloud cover product [Wilson & Jetz 2016], which has been demonstrated to enhance SDMs for species in the Northern Andes. The dataset integrates 15 years of twice-daily remote sensing-derived cloud observations. For our purpose, we used the following parameters: mean monthly cloud frequencies, their mean annual, inter- and intra-annual variability (SD), and the seasonal cloud concentration index. All variables were used at a spatial resolution of 30 arcseconds (approx. 1 sq. km).

Traditional approaches advocate for removing correlated predictor variables before modelling to avoid multicollinearity, which affects model projections [Brun *et al.* 2020]. Generally, suggestions are made to apply different methods (e.g. variance inflation factor, VIF) for mitigating its negative effects [Monge *et al.* 2018; Hanberry 2023a]. The ‘flexsdm’ package offers functions that reduce collinearity in predictors; in our work, however, they were not employed. An exception was made for the method that removes the predictors with a variance inflation factor higher than a selected threshold (in our case, 10). As recently shown, following a standard guideline to remove correlated variables before modelling [Dormann *et al.* 2013] is likely to result in information loss and may end up in incorrect omission of relevant variables to constrain or develop the model, generating bias [Hanberry 2023 b]. Accordingly, the benefits of using all available variables may outweigh the drawbacks of collinearity. Latest research indicates that modelling with correlated climate variables increases the accuracy of predictions [Hanberry 2023b].

### ***Species distribution modelling***

The ‘flexsdm’ R (v. 3.3.3) modelling package [Velazco *et al.* 2022] was used for determining the potential geographic distribution of the proboscis monkey across Sabah. The choice fell on ‘flexsdm’ because of its high manipulation and parametrisation capacity based on different functions and arguments. These attributes enable users to define a complete or partial modelling workflow specific for a modelling situation (e.g. algorithm tuning).

Most SDM methods require either pseudo-absence or background data [Barbet-Massin *et al.* 2012; Wang *et al.* 2023]. Therefore, we used spatial block partitioning to generate pseudo-absence and background points. The calibration area was defined using 5 km buffers around presence points, more than enough to accommodate sizes of group home ranges recorded usually to vary between 1.3 and 9.0 sq. km [Boonratana 2000]. Filtering the occurrence data was used to reduce sample bias by randomly removing points where they were dense (oversampling) in the environmental and geographical spaces. The ‘flexsdm’ package offers a wide range of modelling options. Here, we tested out Maximum entropy (Maxent), one of the most widely used SDM modelling methods [Elith *et al.* 2011]. Maxent can construct simple to highly complex, nonlinear species–environment relationships

using various mathematical transformations of variables (termed features). Six feature classes (FC) are available: linear, quadratic, product, hinge, threshold, and categorical. To reduce overfitting, Maxent uses a regularisation procedure to balance model fit with complexity, by penalising models based on the magnitude of their coefficients [Phillips *et al.* 2006]. Tuned models were built using regularisation multiplier values ranging from 0 to 4 with increments of 0.5, and nine non-categorical FC combinations.

### ***Model evaluation***

Models were evaluated using the area under the receiver operating characteristic curve (AUC) [Swets 1988] and the true skill statistic (TSS) [Allouche *et al.* 2005]. AUC scores range from 0 to 1 (with 0 for systematically wrong model predictions and 1 for systematically perfect model predictions); AUC values 0.7 to 0.8 are considered acceptable. TSS values range from  $-1$  to  $+1$  (with  $-1$  corresponding to systematically wrong predictions and  $+1$  to systematically correct predictions). Because AUC has its drawbacks [Lobo *et al.* 2008], we employed the continuous Boyce index [Boyce *et al.* 2002]. It is continuous and varies between  $-1$  and  $+1$ . Positive values indicate a model that presents predictions consistent with the distribution of presences in the evaluation dataset, values close to zero mean that the model is not different from a random model, and negative values indicate counter predictions [Hirzel *et al.* 2006].

### ***Model interpretability***

A critical challenge in the adoption of machine-learning models is their inherent lack of interpretability, often referred to as the ‘black box’ problem. Shapley Additive exPlanations (SHAP) [Lundberg & Lee 2017; Lin & Gao 2022] represents a significant advancement in addressing this concern by providing a framework for understanding how models arrive at their predictions. SHAP offers various advantages over other variable importance methods, including its interpretability, model-agnostic nature, and ability to consider variable interactions. Leveraging game theory concepts, SHAP provides a robust framework for variable importance attribution in machine-learning models, despite the number of used variables. In this respect, there is no longer a need to remove correlated variables before modeling and benefits of using all available variables can be achieved. The SHAP value quantifies the magnitude and direction of the variable’s influence on the prediction [Lundberg & Lee 2017; Lundberg *et al.* 2018]. The R package ‘shap-values’<sup>2</sup> in a modified version was used to calculate SHAP values for a selected model. A summary plot offers a comprehensive view of the most influential variables in a model and ranks them based on their effect on the model’s predictions. Also, the package can produce SHAP dependence plots, a visualisation tool that helps to understand the relationship between a variable and the model’s prediction. In other words, SHAP values can be integrated into global explanations such as variable importance, but using a completely different from various widely applied so far variable selection methods [Song & Estes 2023].

## **Results and Discussion**

The resulting Maxent model (number of filtered occurrences: 75, regularisation multiplier: 1, FC combinations: linear, quadratic, and hinge) showed excellent performance with a continuous Boyce index of  $0.946 \pm 0.014$  SD and an AUC and TSS of  $0.752 \pm 0.059$  SD and  $0.523 \pm 0.107$  SD, respectively, both of which can be considered good or acceptable. Notably, removing correlated predictor variables failed to improve model performance: the continuous Boyce index amounted to  $0.903 \pm 0.038$  SD, AUC and TSS to  $0.662 \pm 0.108$  SD and  $0.426 \pm 0.141$  SD, respectively.

The SDM was re-classified to areas of low potential habitat suitability, medium and high potential habitat suitability. We defined these thresholds based on Jenks natural breaks, which maximises the similarity of numbers in groups by minimising each class average deviation from the class mean, while maximising each class deviation from the means of the other groups. The Jenks natural break provides a uniform interface to finding class intervals for continuous numerical variables [Jenks &

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<sup>2</sup> <https://github.com/pablo14/>

Caspall 1971]. Under this classification, around 13% of Sabah's territory can be considered highly suitable for the proboscis monkey, where potential suitability is above 0.72 (Fig. 2). As in previous studies mentioned above, our model found a high level of suitability for proboscis monkeys in near-shore areas, most likely restricted to coastal lowland mangrove, riparian, and swamp forests, and along rivers but usually not far from the coast, more inland in dipterocarp forests. In general, this is in line with earlier conclusions, where proboscis monkey populations across Sabah were categorised into seven areas [Sabah Wildlife Department 2019].

Indication of highly suitable for the species inland areas roughly located in the south and south-west of Sabah is perhaps incorrect. Proboscis monkeys seem to avoid such areas. One possible reason for this is that inland forests may not have the necessary dietary minerals<sup>3</sup>. Certain minerals and salts are necessary for their health and well-being and research has shown their strong choice for food plants with high mineral content [Agoramoorthy & Hsu 2005]. The proboscis monkey's preference for coastal mangrove forests and lowland forests near rivers primarily could be due to the higher concentration of essential minerals (e.g. sodium and chloride ions) found in these habitats. In summary, despite the urgency of the situation, the area in Sabah that is highly suitable for proboscis monkeys likely constitutes less than 13% of its total territory, which is a reason for concern.

In our study, we analysed SHAP values to understand the importance of cloud cover variables presumably participating in the governing of the distribution of proboscis monkeys across Sabah. After the original values from the input data have been replaced by SHAP values, the bar plot function of the package 'shap-values' creates a global importance plot, where variable importance is calculated by averaging the absolute SHAP values for each variable across all predictions.

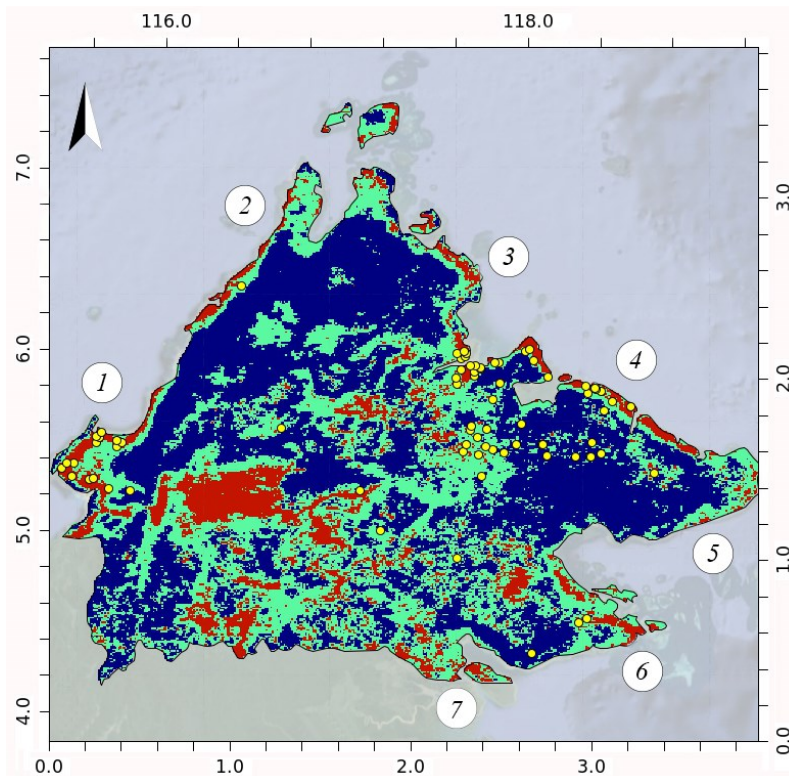


Fig. 2. Jenks natural breaks map of habitat suitability (HS) for proboscis monkeys in areas of Sabah under conditions of cloudiness: red, green, and blue respectively for HS of high (0.72–0.99), medium (0.36–0.72), and low (0.00–0.36) suitability. Yellow dots represent filtered occurrences.

Proboscis monkey populations across Sabah categorised into seven areas: (1) Klias Peninsula, (2) North Sabah, (3) Paitan-Sugut-Beluran, (4) Sandakan-Kinabatangan-Segama, (5) Lahad Datu, (6) Semporna, (7) Tawau-Sebatik island.

Рис. 2. Карта придатності території Сабаха для носачів в аспекті динаміки хмарності, яка отримана методом природних переломів Дженкса: червоним, зеленим та синім позначені території відповідно з високою (0.72–0.99), середньою (0.36–0.72) та низькою (0.00–0.36) придатністю. Жовті точки представляють відфільтровані локалітети знахідок. Номерами 1–7 позначені території концентрації популяцій носачів.

<sup>3</sup> See website: [www.worldlandtrust.org/species/mammals/proboscis-monkey/](http://www.worldlandtrust.org/species/mammals/proboscis-monkey/)

This provides a measure of how important each variable is on average for all predictions. The further a value is from 0, the more influence it will have on the prediction, whereas values near 0 will have less impact on predictions.

As a result, the top five variables have been ranked in the following order: meanAnn (mean annual cloud frequency) > intraAnn (intra-annual variability of cloud frequency, SD) > interAnn (inter-annual variability of cloud frequency, SD) > mean11 (mean cloud frequency for November) > mean02 (mean cloud frequency for February) (Fig. 3). Notably, in this list of cloud cover variables participating in the governing of the distribution of proboscis monkeys across Sabah the mean annual cloud frequency plays a prominent role and is highly negatively correlated with projected habitat suitability (Spearman rank coefficient of correlation estimated as  $-0.83$ ,  $p < 0.01$ ), meaning reduced habitat suitability is accompanied by increased cloudiness.

By adding a regression option to the ‘shap-values’ R script, the SHAP dependence plot function produces a hump-shaped curve revealing the relationship between mean annual cloud frequency and the model’s prediction. Under this relationship, habitat suitability reaches its maximum at mean annual cloud frequency of around 70%, after which it sharply declines. In this respect, there is strong evidence showing how cloud cover modulates irradiance thus limiting photosynthesis, affecting fruit and flower production, as well as plant development [Zimmerman *et al.* 2007; and others], thereby deeply determining the quality of the monkey’s habitat.

Next in the list of most contributing to the model variables are those characterising the intra- and interannual variability of cloud frequency. Indeed, cloud cover can vary seasonally and from year to year, with some periods experiencing more cloudiness than others do. Near the equator, seasonal changes in cloud cover are considered a more important cause than seasonal changes in day length and solar angle [Miller & Feddes 1971]. This is likely to influence the overall light environment in the forest and impact the growth and distribution of different tree species, and also affect fruit and flower production. Finally, mean cloud frequencies for November and February fall into the category of influential variables, most probably because of their heavy cloudiness.

While irradiance is a critical factor limiting plant performance in many tropical forests, cloudiness can modify this relationship in significant ways. Understanding the interactions between cloudiness, irradiance, and plant performance is essential for predicting the future of tropical forest ecosystems and their role as proboscis monkey habitat in the face of climate change. A recent study hypothesised that deforestation of natural primary forests in Borneo and replacing them with single tree species (palm tree) may cause larger variability from the normal cloud and climate states over the area [Punay & Andinisari 2022].

The conversion of Borneo’s forests to oil palm plantations can have a significant impact on cloud properties. These changes can lead to reduced rainfall and increased risk of drought [McAlpine *et al.* 2018]. This is a critical issue with far-reaching consequences for both the environment and the wildlife in and around Borneo, including the proboscis monkey population of Sabah.

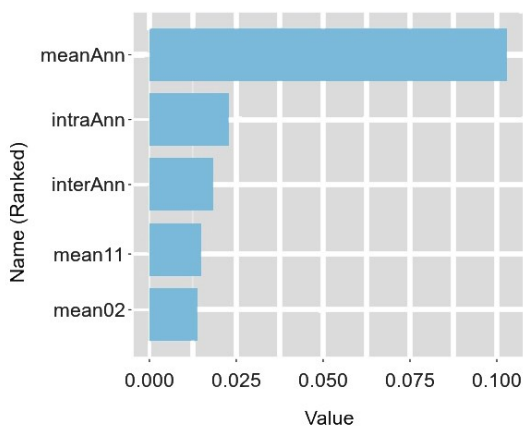


Fig. 3. Summary plots of the average absolute SHAP values of the five most contributing to the model variables. The y-axis represents variables used in the study (see text). The x-axis represents the corresponding SHAP value.

Рис. 3. Зведені графіки середніх абсолютних значень SHAP для п’яти найбільш значимих змінних моделей. Вісь Y представляє змінні, що використовуються в дослідженні (див. текст). Вісь X представляє відповідне значення SHAP.

## Conclusions

This study aimed to model the distribution and habitat suitability for the endangered proboscis monkey species in its native ecosystem in Sabah (Borneo) using a Maximum entropy (Maxent) approach to species distribution modelling. Under this task, we specifically placed emphasis on the effect of environmental parameters such as cloud cover. Model evaluation gave satisfactory results. Our model found a high level of habitat suitability for proboscis monkeys in nearshore areas. Based on the resulting SDM, three distinct classes ranging from low to high suitability values were identified. One alarming conclusion from this exercise is that habitats suitable for proboscis monkeys in Sabah make up less than 13% of the state's total area, raising concerns about their long-term survival. In terms of environmental causes, cloud cover, especially average annual cloudiness, is a major factor in determining where proboscis monkeys can be found thriving in Sabah. Unfortunately, the conversion of Borneo's forests to palm oil plantations can have a significant negative impact on cloud properties.

## Declarations

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**Conflict of interests.** The author has no conflicts of interest to declare that are relevant to the content of this article.

**Handling of materials.** All manipulations with living animals were carried out using non-lethal techniques and in compliance with the current legislation of Ukraine.

## References

- Agoramoorthy, G., M. J. Hsu. 2005. Borneo's proboscis monkey — A study of its diet of mineral and phytochemical concentrations August 2005. *Current Science*, **89** (3): 454–457.
- Allouche, O., A. Tsoar, R. Kadmon. 2006. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.*, **43**: 1223–1232. [CrossRef](#)
- Atmoko, T., Mukhlisi. 2021. The Conservation of Proboscis Monkey in Suwi River, East Kalimantan, Indonesia. *BIO Web Conf.*, **33**: 01004. [CrossRef](#)
- Barbet-Massin, M., Jiguet, F., Albert, C. H., Thuiller, W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods Ecol. Evol.*, **3**: 327–338. [CrossRef](#)
- Bennett, E., A. C. Sebastian. 1988. Social organization and ecology of proboscis monkey (*Nasalis larvatus*) in mixed coastal forest in Sarawak. *International Journal of Primatology*, **9**: 233–255. [CrossRef](#)
- Bennett, E. L., F. Gombek. 1993. Proboscis monkeys of Borneo. *Natural History Publications (Borneo)*. Sdn. Bhd. & Koktas Sabah, Ranau, Sabah, Malaysia, 84–99.
- Bernard, H. 1997. A study on the distribution and abundance of proboscis monkey (*Nasalis larvatus*) in the Klias Peninsula, Sabah, North Borneo. *Journal of Wildlife Management & Restoration in Sabah*, **1**: 1–12.
- Boonratana, R. 1993. *The ecology and behaviour of the proboscis monkey (Nasalis larvatus) in the Lower Kinabatangan, Sabah*. PhD Thesis, Faculty of Graduate Studies, Mahidol University, Thailand, 1–183.
- Boonratana, R. 2000. Ranging Behavior of Proboscis Monkeys (*Nasalis larvatus*) in the Lower Kinabatangan, Northern Borneo. *International Journal of Primatology*, **21** (3): 497–518. [CrossRef](#)
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecol. Model.*, **157**: 281–300. [CrossRef](#)
- Brun, P., W. Thuiller, Y. Chauvier, L. Pellissier, R. O. Wüest, [et al.]. 2020. Model complexity affects species distribution projections under climate change. *Journal of Biogeography*, **47** (1): 130–142. [CrossRef](#)
- Chapman, A. D. 2005. *Principles and Methods of Data Cleaning — Primary Species and Species Occurrence Data, version 1.0*. Report for the Global Biodiversity Information Facility, Copenhagen, 1–75.
- Chapman, C. A., C. A. Peres. 2001. Primate conservation in the new millennium: The role of scientists. *Evol. Anthropol.*, **10**: 16–33. [CrossRef](#)
- Davies, G., J. Payne. 1982. *A faunal survey of Sabah. Report, IUCN/WWF Project No.1692*, WWF–Malaysia, Kuala Lumpur.
- Dormann, C.F., J. Elith, S. Bacher, C. Buchmann, G. Carl, [et al.]. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36** (1): 27–46. [CrossRef](#)
- Elith, J., J.R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, **40**: 677–697. [CrossRef](#)
- Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, C. J. Yates. 2011. A statistical explanation of maxent for ecologists. *Diversity and Distributions*, **17**: 43–57. [CrossRef](#)
- Fois, M., A. Cuena-Lombrana, G. Fenu, G. Bacchetta. 2018. Using species distribution models at local scale to guide the search of poorly known species: Review, methodological issues and future directions. *Ecological Modelling*, **385**: 124–132. [CrossRef](#)
- Fuller, D. O., T. C. Jessup, A. Salim. 2004. Loss of forest cover in Kalimantan, Indonesia, since the 1997–1998 El Niño. *Conserv. Biol.*, **18** (1): 249–254. [CrossRef](#)
- GBIF Occurrence*. GBIF.org, 28 July 2024. [CrossRef](#)
- Gerstner, B. E., M. E. Blair, P. Bills, C. A. Cruz-Rodriguez, P. L. Zarnetske. 2024. The influence of scale-dependent geodiversity on species distribution models in a biodiversity hotspot. *Philos Trans A Math Phys Eng Sci.*, **382** (2269): 20230057. [CrossRef](#)
- Guisan, A., W. Thuiller. 2005. Predicting species distribution:



- Offering more than simple habitat models. *Ecology Letters*, **8**: 993–1009. [CrossRef](#)
- Guisan, A., N. E. Zimmermann. 2000. Predictive Habitat Distribution Models in Ecology. *Ecological Modelling*, **135**: 147–186. [CrossRef](#)
- Hanberry, B. B. 2023a. Practical guide for retaining correlated climate variables and unthinned samples in species distribution modeling, using random forests. *Ecological Informatics*, Available online 2.12.2023, 102406. [CrossRef](#)
- Hanberry, B. B. 2023b. Shifting potential tree species distributions from the Last Glacial Maximum to the Mid-Holocene in North America, with a correlation assessment. *J. Quaternary Sci.*, **38**: 829–839. [CrossRef](#)
- Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, **199**: 142–152. [CrossRef](#)
- Jenks, G. F., F. C. Caspall. 1971. Error on choroplethic maps: definition, measurement, reduction. *Ann. Assoc. Am. Geogr.*, **61**: 217–244. [CrossRef](#)
- Kawabe, M., T. Mano. 1972. Ecology and behavior of the wild proboscis monkey, *Nasalis larvatus* (Wurmb), in Sabah, Malaysia. *Primates*, **13**: 213–227. [CrossRef](#)
- Lin, K., Y. Gao. 2022. Model interpretability of financial fraud detection by group SHAP. *Expert Systems with Applications*, **210**: 118354. [CrossRef](#)
- Lobo, J. M., A. Jiménez-Valverde, R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, **17**: 145–151. [CrossRef](#)
- Lundberg, S. M., S. I. Lee. 2017. A unified approach to interpreting model predictions. In: *Proceedings of the 31st International Conference on Machine Learning*, 3547–3555.
- Lundberg, S. M., B. Nair, M. S. Vavilala, M. Horibe, M. J. Eisses, [et al.]. 2018. Explainable machine-learning predictions for the prevention of hypoxaemia during surgery. *Nature biomedical engineering*, **2** (10): 749–760. [CrossRef](#)
- McAlpine, C. A., A. Johnson, A. Salazar, J. Syktus, K. Wilson, [et al.]. 2018. Forest loss and Borneo's climate. *Environmental Research Letters*, **13** (4): 044009.
- Medway, L. 1977. Mammals of Borneo. Field keys and annotated checklist. *Monographs of the Malaysian Branch of the Royal Asiatic Society*, **7**: i–xii, 1–172.
- Meijaard, E., V. Nijman, J. Supriatna. 2008. *Nasalis larvatus*. *The IUCN Red List of Threatened Species 2008*: e.T14352A4434312.
- Meijaard, E., V. Nijman. 2000. Distribution and conservation of the proboscis monkey (*Nasalis larvatus*) in Kalimantan, Indonesia. *Biological conservation*, **92** (1): 15–24. [CrossRef](#)
- Miller, D. B. R. G. Feddes. 1971. *Global Atlas of Relative Cloud Cover, 1967–70: Based on Data from Meteorological Satellites*. US National Environmental Satellite Service, USAF Environmental Technical Applications Center, 1–237.
- Monge, M. J., R. García-Valdés, R. Sánchez-Fernández, M. Acevedo. 2018. Evaluating collinearity effects on species distribution models: An approach based on virtual species simulation. *PLoS One*, **13** (5): e0196463. [CrossRef](#)
- Napier, J. R., P. H. Napier. 1967. *A Handbook of Living Primates*. Academic Press, London, 1–456.
- Pacayán, S., F. D. Alfaro, W. Pérez-Martínez, I. Briceño-de-Urbaneja. 2019. Potential distribution model of *Leontochir ovallei* using remote sensing data. *Revista de Teledetección*, (54): 59–69. [CrossRef](#)
- Payne, J. 1988. *Orang-utan Conservation in Sabah, WWF Malaysia*. Project No. 96/86 and WWF International Project No. 3759. WWF Malaysia, Kuala Lumpur, 1–137.
- Phillips, S. J., R. P. Anderson, R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**: 231–259. [CrossRef](#)
- Punay, J.P., R. Andinisari. 2022. Review: land, cloud, and climate change (in focus: Borneo). *Journal of Infrastructure Planning and Engineering (JIPE)*, **1** (1): 33–37. [CrossRef](#)
- Sabah ... 2019. *Sabah Wildlife Department 2019. Proboscis Monkey Action Plan for Sabah 2019–2028*. Kota Kinabalu, Sabah, Malaysia, 1–42.
- Sakti, A., K. Adillah, C. Santoso, I. Al Faruqi, V. S. Adi Hendrawan, [et al.]. 2024. Modeling Proboscis Monkey Conservation Sites on Borneo Using Ensemble Machine Learning. *Global Ecology and Conservation*, **54**: e03101. [CrossRef](#)
- Salter, R. E., N. A. MacKenzie, N. Nightingale, K. M. Aken, P. K. P. Chai. 1985. Habitat use, ranging behaviour, and food habits of the proboscis monkey, *Nasalis larvatus* (van Wurmb), in Sarawak. *Primates*, **26**: 436–451. [CrossRef](#)
- Salter, R. E., N. A. MacKenzie. 1985: Conservation status of the proboscis monkey in Sarawak. *Biological Conservation*, **332**: 119–132. [CrossRef](#)
- Sha, J. C. M., H. Bernard, S. Nathan. 2008. Status and conservation of proboscis monkeys (*Nasalis larvatus*) in Sabah, East Malaysia. *Primate Conservation*, (23): 107–120. [CrossRef](#)
- Song, L., L. Estes. 2023. itsdm: Isolation forest-based presence-only species distribution modelling and explanation in R. *Methods in Ecology and Evolution*, **14**: 831–840. [CrossRef](#)
- Swets, J. A. 1988. Measuring the Accuracy of Diagnostic Systems. *Science*, **240**: 1285–1293. [CrossRef](#)
- Toulec, T., S. Lhota, H. Soumarová, A. Kurniawan, S. Putera, W. Kustiawan. 2020. Shrimp farms, fire or palm oil? Changing causes of proboscis monkey habitat loss *Global Ecology and Conservation*, **21**: e00863. [CrossRef](#)
- Velazco, S. J. E., M. B. Rose, A. F. A. Andrade, I. Minoli, J. Franklin. 2022. flexsdm: An R package for supporting a comprehensive and flexible species distribution modelling workflow. *Methods in Ecology and Evolution*, **13** (8): 1661–1669. [CrossRef](#)
- Wang, X., Q. Xu, J. Liu. 2023. Determining representative pseudo-absences for invasive plant distribution modeling based on geographic similarity. *Front. Ecol. Evol.*, 19 June 2023, *Sec. Models in Ecology and Evolution*, 11. [CrossRef](#)
- Wilson, A. M., W. Jetz. 2016. Remotely sensed high-resolution global cloud dynamics for predicting ecosystem and biodiversity distributions. *PLoS Biol.*, **14** (3): e1002415. [CrossRef](#)
- Wolfheim, J. H. 1983. *Primates of the World: Distribution, Abundance and Conservation*. Univ. Washington Press, Seattle & London, i–xxiii + 1–831.
- Yeager, C. P., 1989. Proboscis monkey (*Nasalis larvatus*) feeding ecology. *Int. J. Primatol.*, **10**: 497–530. [CrossRef](#)
- Zimmerman, J. K., S. J. Wright, O. Calderón, M. A. Pagan, S. Paton. 2007. Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of annual changes in irradiance. *Journal of Tropical Ecology*, **23** (2): 231–251. [CrossRef](#)