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The endangered red panda in Himalayas: Potential distribution and ecological habitat associates

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ABSTRACT

The red panda *Ailurus fulgens*, an endangered herbivorous member of the order Carnivora that is endemic to the eastern Himalayan broadleaf and coniferous forests, is surviving under threats induced by human activity and climate change. The distribution range of the red panda in Nepal represents an understudied remnant population at the edge of its western biogeographic distribution range. To build a potentially suitable habitat, we used red panda occurrence and the least correlated bioclimatic variables in MaxEnt modeling. In addition, habitat variables were recorded in transects and quadrat plots to identify ecologically important variables for the red panda habitat. Currently, 14.23% (21,680 km^2) of Nepal is a climatically suitable habitat for the red panda. The mean temperature of the warmest quarter, annual temperature range, mean temperature of the coldest quarter and precipitation of the coldest quarter are the major contributing variables in the model, with an area under the ROC curve (AUC) of 0.94. Climatic, geographic, and habitat group variables have considerable contributions, while disturbance has a low contribution. Multiple factor analysis identified mixed broadleaf forest, East Himalayan oak-laurel forest, canopy cover >20%, ground substrate use, bamboo cover >20%, tree stump presence, fallen logs of small trees and habitat without grazing as having high contributions in the qualitative groups. Similarly, the elevation, distance from settlements and roads, distance to water sources, annual temperature range, mean diurnal range and annual precipitation were important variables in the quantitative groups. The results will help guide conservation managers in implementing effective habitat management programs for the red panda.

1. Introduction

Understanding the environmental and anthropogenic factors that influence the distribution and abundance of wildlife is a major concern in ecological research. Proper understanding of habitat components and their management are key tools for

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protecting wildlife in various conservation regimes (Khadka and James, 2016). A habitat is engineered through the interactions of several environmental factors in a multidimensional space (Madhusudan and Johnsingh, 1998). A combination of the altitude, aspect and slope of topographically complex mountains (Srivastava and Kumar, 2018) and other associated factors, including precipitation, humidity and the soil nutrient content, influence the abundance and quality of forage for different wildlife. Vegetation patches in the forest understory, such as bamboo, are an important food resource for many wild herbivores, particularly specialists, such as the red panda (Yonzon, 1989; Pradhan et al., 2001; Thapa and Basent, 2015). These patches also provide quality forage resources for livestock in transhumant pastoral systems. Both physical and biotic factors have key roles in shaping species distributions (Benton, 2009), and thus, the factors that determine habitat selection are numerous and differ from one species to another. Exploration, identification, and understanding of the key habitat components that limit species distributions are paramount to effective wildlife management (Morrison et al., 2006).

The red panda *Ailurus fulgens*, an herbivorous mammal from the order Carnivora, is an endemic species to the eastern Himalayan broadleaf and coniferous forests. Due to its unique habitat requirements, the red panda is recognized as a habitat and dietary specialist that primarily depends on a bamboo diet and dwells in bamboo understories in temperate coniferous forests adjacent to broadleaf forests (Yonzon and Hunter, 1991). Currently, the red panda is distributed in the five Asian countries of Nepal, India, Bhutan, northern Myanmar, and China (Yonzon, 1989; Reid et al., 1991; Wei et al., 1998, 1999; Choudhury, 2001; Pradhan et al., 2001; Dorji et al., 2012; Bista et al., 2017). Despite its wide geographic range across the Himalayas, the red panda occurs at low densities in fragmented and isolated forest patches under high anthropogenic pressure (Yonzon and Hunter, 1991; Williams, 2003; Jnawali et al., 2012; Sharma et al., 2014; Bista et al., 2017; Panthi et al., 2017). Less than 10000 individuals are believed to remain in the wild in isolated and declining populations, and classified as the endangered species on the International Union for Conservation of Nature's Red List (Glatston et al., 2015). Habitat loss, fragmentation and degradation are the major threats to red pandas in the wild across their entire range, and other associated anthropogenic disturbances (e.g., grazing, resource collection, development activities) increasingly aggravate the situation (Wei et al., 1999; Glatston et al., 2015; Thapa et al., 2018). Varying in climate and topography, the red panda habitat is composed of a wide range of forests types with bamboo thicket understories (Yonzon et al., 1991a; Wei et al., 1999). Within different forest types, the red panda prefers steeper slopes, higher densities of fallen logs, tree stumps, shrubs, bamboo culms, bamboo cover, canopy and close proximity to water sources (Yonzon, 1989; Pradhan et al., 2001; Zhang et al., 2006, 2011; Dorji et al., 2012; Zhou et al., 2013). An appropriate understanding of these habitat covariates helps to determine a habitat's suitability for the red panda.

Studies on the distribution and habitat ecology of the red panda are essential components to species-specific conservation efforts (Thapa et al., 2018). These studies have been conducted sparsely and in small geographic areas, resulting in inadequate information for capturing wider habitat requirements and hampering the implementation of large-scale habitat management and protection measures. In 2015 and 2016, field surveys were conducted in the primary red panda habitat in Nepal, covering the following protected areas (PAs): Rara National Park (RNP), Langtang National Park (LNP), Gaurishankar Conservation Area (GCA), Dhorpatan Hunting Reserve (DHR) and outside protected areas (Panchthar-Ilam-Taplejung community forest), encompassing a wide range of habitats in western, central and eastern Nepal. There are distinct climatic conditions and complex topography throughout the country. The vegetation composition, particularly the forest type, differs between the western and eastern regions, with higher annual precipitation in the east. Such broad habitat conditions provide habitats for many endangered species. Transhumant pastoralism supports the subsistence livelihoods of mountain communities in Nepal and simultaneously increases pressure on forests and alpine meadows (Khadka and James, 2016). In a pastoral system, livestock shelters are temporary and move across pastures and forests (Fox et al., 1996), which are considered potential habitats for many species, including the red panda (Bista et al., 2017). Furthermore, wildlife in mountain PAs, including LNP, GCA, DHR, and RNP, is threatened by livestock grazing pressure in Nepal (Yonzon and Hunter, 1991; Sharma et al., 2014; Panthi et al., 2017). A previous study in RNP reported that the presence of the red panda is adversely affected by livestock grazing (Sharma et al., 2014). An increasing human population and equally fast-paced development activities (road construction, e.g., in Panchthar-Ilam-Taplejung in the east, and high-altitude hydropower projects, e.g., in GCA in central Nepal) utilize a considerable amount of natural resources and affect biodiversity at local levels. To direct effective and efficient efforts for red panda conservation, an understanding of its habitat requirements is essential at both fine and large scales and for determining its distribution. We hypothesized that distribution of red panda is associated with both local and broad scale factors. This study aimed to determine the potential distribution and identify the key habitat features that influence the distribution of the red panda on a broad scale. The outcomes of this study are expected to aid management authorities in implementing better long-term conservation measures.

2. Materials and methods

2.1. Study area

This study was conducted in four PAs that contain the largest portion of suitable habitats for the red panda in Nepal. This study included a wide geographical range, capturing part of the western, central and eastern regions of the country. This range encompasses RNP and DHR in the western region, LNP and GCA in the central region, and PIT (Panchthar-Ilam-Taplejung community forest) in the far eastern part of Nepal (Fig. 1).

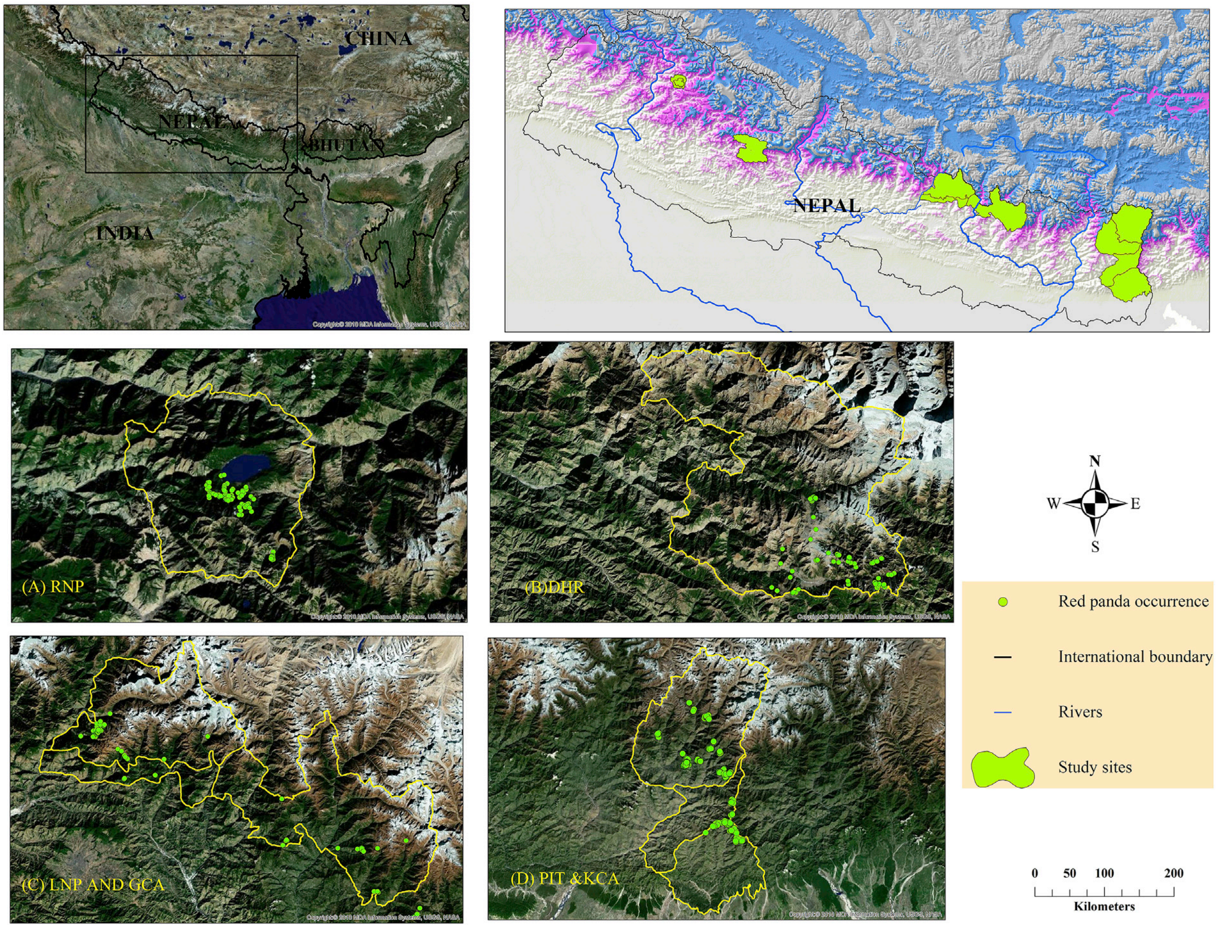

Fig. 1. Study area. Rara National Park (RNP) (a) and Dhorpatan Hunting Reserve (DHR) (b) in western Nepal; Langtang National Park (LNP) and Gaurishankar Conservation Area (GCA) (c) in central Nepal; and PIT community-managed forest in eastern Nepal (d). Green dots represent red panda occurrence records.

2.2. Data collection

Previous studies have used feces as an effective indicator of species occurrence due to a limited chance of sightings (Wei et al., 2000; Zhang et al., 2004). Usually the red pandas leave shiny greenish feces in a group (8–15 pellets in single), which sometimes used repeatedly in a single consisting 15–30 pellets or sometimes more than 100. It makes easy to distinguished feces of red panda from other species. A completely random sampling approach is infeasible due to the steep mountain terrain (Qi et al., 2009). Due to limited time and logistical constraints, we adopted stratified random sampling combined with random line transects in the field representing all habitat types. In the field, observers walked transects, which ranged between 0.5 and 1.5 km, with a width of 10 m (limitations in the transect length were based on the topographic steepness and rocky slopes), across the species' elevation range (2200 m–4000 m) to record red panda signs (feces). In total, 81 transects (RNP = 19, DHR = 14, LNP = 14, GCA = 13, PIT = 21) and 320 plots (western = 120, central = 110, eastern = 90) were surveyed in the field. When feces was encountered, the point location was geo-referenced with a handheld Global Positioning System and habitat variables were recorded in plots with a predetermined size (20 m × 20 m) (Wang et al., 2009). The following habitat variables were recorded: elevation, slope aspect, substrate use, vegetation type, forest status, canopy cover, fallen logs, poaching signs, fire, firewood collection, bamboo cover, cut stumps, and distance to water sources, settlements, and roads. Additionally, based on the coverage of bamboo in a 1 m × 1 m plot, the bamboo cover in the plot was visually estimated in the field and then assigned to one of four categories (>1%, 1–24%, 50–74%, <74%) (Taylor and Zisheng, 1993). In all, 19 freely available bioclimatic variables (temperature and precipitation) and elevation data (derived slope and aspect) were downloaded from WorldClim (Hijmans et al., 2005). The variables were assigned to one of four groups that were considered to be major environmental variables for the red panda: habitat, geography, climate and disturbance (Thapa et al., 2018) (Table S1).

2.3. Species distribution modeling

The maximum entropy algorithm (MaxEnt 3.3.3k) is one of the most robust bioclimatic modeling approaches for presence-only data (Elith et al., 2006b, 2011; Wisz et al., 2008), and the program was implemented to build the distribution of current suitable habitats in Nepal. Red panda occurrence data were collected during field surveys in 2015 and 2016 based on signs (feces) and direct sightings in transects. All of these presence records ($N = 320$) covered spatially distinct geographic areas of western, central and eastern Nepal (Fig. 1). MaxEnt randomly removes species records when multiple occurrences are recorded within a grid. All 19 bioclimatic variables were downloaded from the WorldClim website (http://www.worldclim.org) (Hijmans et al., 2005). The extent was set as the whole boundary of Nepal with a model resolution of 30 arc seconds. After removing highly correlated variables (correlation coefficients ≥ 0.75) (Table S2) and variables that did not contribute to the model, the following variables were included in the climate model: the mean temperature of the warmest quarter, annual temperature range, mean temperature of the coldest quarter, precipitation of the coldest quarter, precipitation of the warmest quarter, precipitation of the driest month, and mean diurnal range. The model outputs were converted into a binary map using the logistic threshold methods, which maximize the sum of the sensitivity and specificity (Liu et al., 2013); these methods are an inbuilt functionality of MaxEnt. The model predictive ability was tested with twenty-fold cross-validations and comparisons based on the area under curve (AUC) of the receiver operator characteristics (ROC) curve (Fig. S1). The training and test AUC above 0.75 indicated a reasonable to high model discrimination ability and good model performance (Elith et al. 2006a,b).

2.4. Multiple factor analysis

The distribution of red panda signs based on elevation, aspect, substrate use and forest types is presented in bar plots for the different study sites. Based on the nature of the data (qualitative and quantitative), all variables were separated into four groups: habitat, geography, disturbance and climate (Table S1). Multiple factor analysis (MFA) was chosen among the variety of symmetric ordination methods that are available for linking ecological data tables (Dray et al., 2003) because this method allows for the simultaneous coupling of several groups or subsets of variables defined by the same objects (Escofier and Pages, 1994). MFA is considered a principal component analysis (PCA) when the variables are quantitative (here, geographic and climatic variables) and multiple correspondence analysis (MCA) is performed with qualitative variables (here, habitat and disturbance variables). In this study, the coordination among all groups (habitat, geography, climate and disturbance) was evaluated via MFA (Pagès, 2002) using the “MFA” function in the FactoMineR package (Lê et al., 2008). To determine the ability of MFA to predict the presence/absence of red panda signs, logistic regression models were built using the first five dimensions of MFA following the backward elimination technique.

3. Results

3.1. Predicting potential habitats for the red panda

The training AUC and test AUC of the distribution model were 0.96 and 0.94, respectively (Fig. S1), indicating that the model performed better than random. The total potential climatically suitable habitat for red panda was determined to be 21,680 km^2, which represents 14.73% of the total area of Nepal. The distribution model indicates that the red panda habitat is currently distributed across eastern and western Nepal. The model clearly showed that the eastern region (comprising the central and eastern parts of the country) comprises the largest suitable habitat for the red panda (Fig. 2). Out of eight least correlated predictors, the mean temperature of the warmest quarter, annual temperature range, mean temperature of the coldest quarter, and precipitation of the coldest quarter had higher contributions that accounted for over 90% of the model performance. The current distribution of the red panda habitat is highly influenced by the mean temperature of the warmest quarter (41.6%), followed by the annual temperature range, mean temperature of the coldest quarter, precipitation of the coldest quarter and precipitation of the warmest quarter (Fig. 3). Additionally, the Jackknife test showed that the mean temperature of the warmest quarter, annual temperature range, mean temperature of the coldest quarter and precipitation of the coldest quarter were the main variables (Fig. S2). Response curves showed the quantitative relationship between the logistic probability of the presence and environmental variables, and deepened the understanding of the ecological niche of the red panda (Fig. S8).

3.2. Distribution of red panda signs

Red panda signs were recorded in the elevation range between 2400 and 3800 m with an average of 3200 ± 300 m in Nepal. The distribution of signs among sites was significantly different ($F = 101.78$, $df = 4$, $P < 0.005$). Central Nepal, including LNP and GCA, recorded feces at a higher elevation compared to eastern Nepal (Fig. S3). Red pandas were mainly observed defecating on the ground or forest floor, fallen logs, tree branches and rock (Fig. S3B). The ground or forest floor was the preferred site for defection ($\chi 2 = 91.58$, $df = 3$, $p < 0.001$). A large proportion of sign occurrence was observed in the NE (northeast) (28%), followed by the NW (24%), N (15%), W (14%) and at very low percentages in the remaining aspects (Fig. S4A). There was a significant difference in the proportion of signs observed among the aspects ($\chi 2 = 219.02$, $df = 7$,

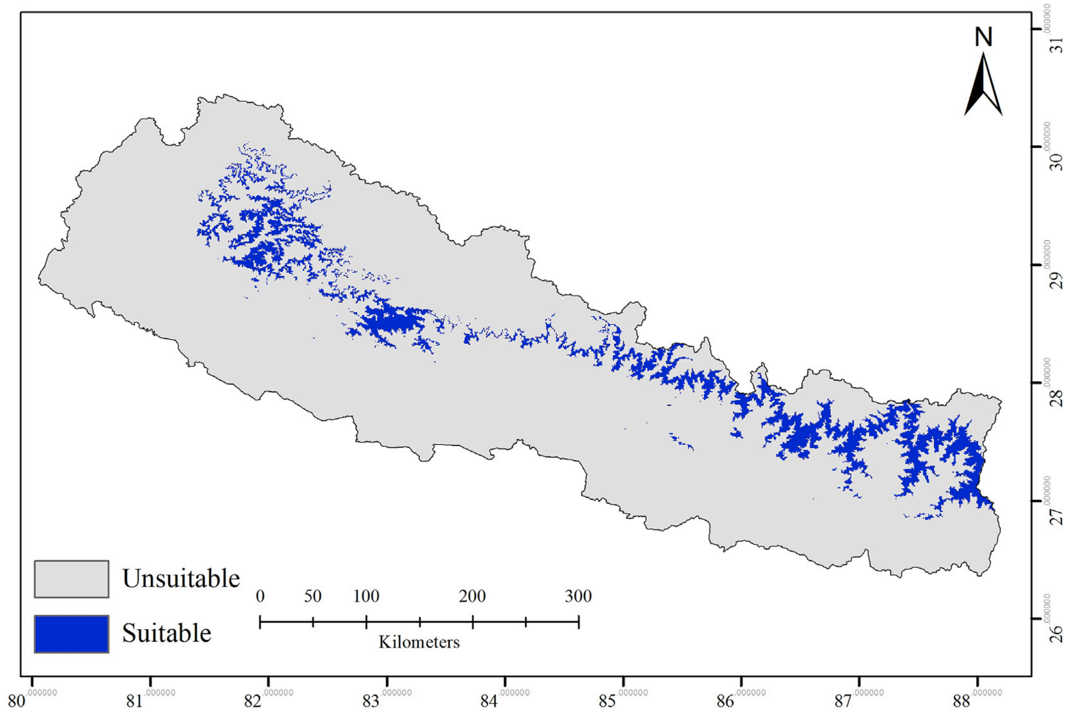

Fig. 2. Distribution of the potential habitat of the red panda in the Nepal Himalayas.

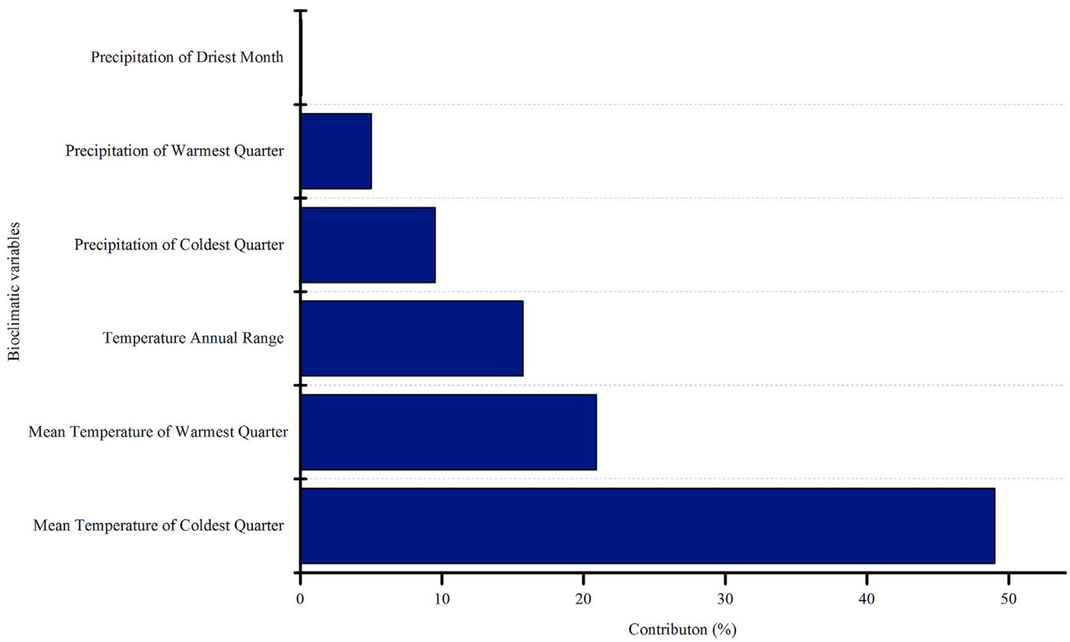

Fig. 3. Relative contributions of selected bioclimatic variables in the model.

$p < 0.001$). Among forest types, the highest number of signs was observed in the fir forest (FIRF; 34%), followed by the temperate mountain oak forest (TMOF; 13%), and mixed broadleaf forest (MBLF; 10%); very few signs were observed in other forest types (Fig. S4B). The proportion of observed signs among the forest types was significantly different ($\chi 2 = 239.38$, $df = 9$, $p < 0.001$).

3.3. Habitat association in relation to group and individual covariates

Four groups of variables, namely, habitat, geography, climate and disturbance, consisting of both quantitative and qualitative environmental variables, of the red panda habitat were analyzed using MFA. The highest eigenvalue obtained showed that 21 dimensions were required to capture all of the data variations. By visualizing the screen plot and variance, at least five dimensions were required to retain 36% of the variance in the data. The first two dimensions of this space were plotted to examine the association among the group variables in the red panda habitat. Dimension 1 accounted for 12.2% of the variance in the data and dimension 2 accounted for 7.4% of the variance (Fig. 4). The climatic, geographic, and habitat groups had high contributions in dimension 1, but disturbance had a low contribution (Table 1). Overall, the habitat and geographic variables had a high contribution in all five dimensions (Dim. 1–5), indicating these variables as majorly influential environmental groups in the red panda habitat. Climatic and disturbance had slightly lower contributions in all dimensions (Dim. 1–5) compared with the other groups and were positively associated with the red panda habitat. Furthermore, the correlation between groups and dimensions plots showed that three group variables (climate, geography and habitat) had similar contributions in the first dimension, indicating that they had almost identical influences; however, disturbance was correlated with dimension 2 and had the least influence among all of the group variables (Fig. S5).

In a similar ordination space, by examining the effect of the individual variables in categorical groups, forest type, canopy cover, substrate use and bamboo cover had a high contribution to red panda occurrence across the study sites. These variables were significant in habitat selection of the red panda. For qualitative variables, the top eight highest contributing variables were mixed broadleaf forest (MBLF), canopy cover (canopy_1 > 20%), ground substrate use (subs_0), bamboo cover (bamc_1), East Himalayan oak-laurel forest (EHOLF), grazing (graz_1), tree stumps (ctstmp_0) and fallen logs (fall.log_0) (Fig. S6). Within the quantitative group, the variables of climate and geographic elevation, distance to settlements (increasing distance), distance to roads (increasing distance), annual temperature range (bio7), mean diurnal range (bio2) and annual precipitation (bio12) had a high contribution in dimension 1. In dimension 2, geographic variables (slope, aspect, elevation, and distance to settlement) had a higher contribution than climatic variables. In dimensions 4 and 5, distance to water (closer distance) had a high contribution.

Logistic regression models were built to predict the probability of occurrence of red panda signs based on the MFA dimensions. The results showed that four dimensions (Dim. 1, 2, 3, and 5) were highly significant predictors of occurrence probability of the red panda, with Dim 1 and Dim 2 having greater significance (Table S3 and Fig. S7). The slopes of three dimensions were negative, indicating that the probability of occurrence favored habitat, climate and geographic group variables.

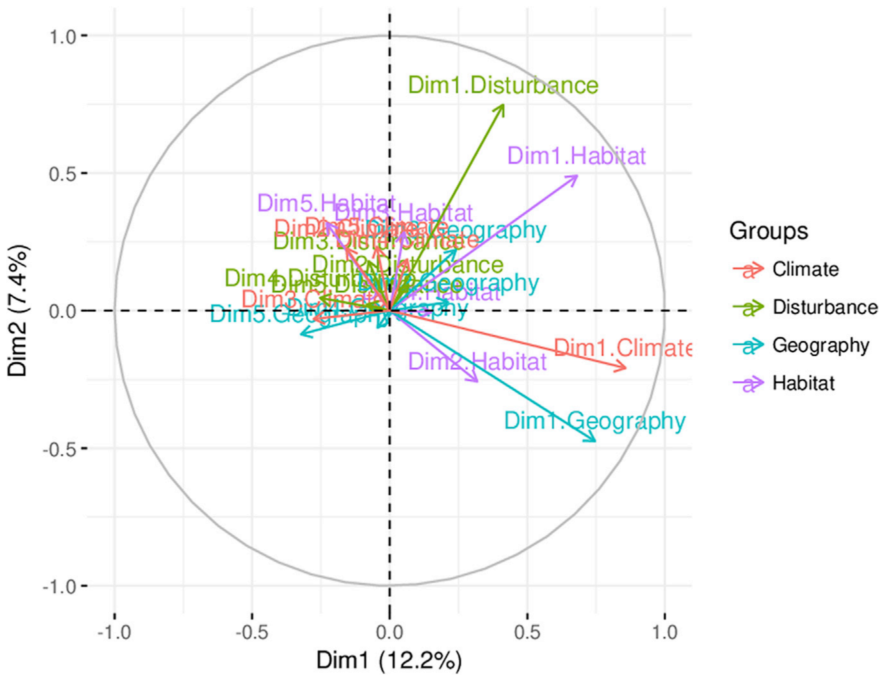

Fig. 4. Ordination plot from MFA based on the climate, disturbance, geographic and habitat groups. The graph of partial axes shows the relationship between the principal axes of MFA and those obtained from analyzing each group using either PCA (for groups of quantitative variables: climate and geography) or MCA (for qualitative variables: habitat and disturbance).

Table 1
Dimension loading in four groups in MFA. Only the first five dimensions are shown.

Variable Group	Dim. 1	Dim. 2	Dim. 3	Dim. 4	Dim. 5
Habitat	27.8936	33.6802	34.2223	32.5299	30.3946
Disturbance	9.51777	42.1131	11.4922	26.3974	17.9934
Geography	29.5981	19.2000	29.4852	30.8708	46.1755
Climate	32.9905	5.0066	24.8001	10.2017	5.43629

4. Discussion

4.1. Potentially suitable habitat of the red panda

This study elucidated the current distribution of the climatically suitable habitat for the red panda at the edge of its western biogeographical distribution range boundary in Nepal. Our results determined that a larger area is climatically suitable for the red panda in Nepal than its current distribution, which is similar to the current known occurrence records. The current potentially suitable habitat is concentrated in the eastern region. Eastern Nepal is part of the eastern Himalayas, where the red panda is endemic to broadleaf and coniferous forests(Williams, 2003). In addition, climatic variation and topographic complexity make the eastern Himalayas a rich biodiversity hotspot globally and a favorable habitat for a wide array of species (Sharma et al., 2010), including the endangered red panda. The eastern Himalayas have high humidity levels, favor the growth of diverse vegetation, including bamboo species, the primary food of the red panda. The current potential habitat of the red panda is distributed in a narrow altitudinal range between 2100 m and 4000 m, indicating that the majority of the habitat occurs at an altitude of 3000 m. This result is similar to studies on the red panda in different areas of Nepal by (Yonzon, 1989; Williams, 2003; RPN, 2010; Jnawali et al., 2011; Bhatta et al., 2014; Thapa et al., 2014; Thapa et al., 2018). Our model-predicted habitat is 21,680 km^2, which agrees with previous studies by Kandel et al. (2015) and Mahato (2010), those studies have predicted across the landscape. Kandel et al. (2015) suggested that the red panda habitat in Nepal should be a focal area for the conservation of the subspecies *Ailurus fulgens* in the Himalayas. Choudhury (2001) may have underestimated the habitat at only 8200 km^2 which has large difference with our study that might due difference in methodological approaches. By contrast, Yonzon et al. (1997) and Jnawali et al. (2012) estimated only 912 km^2 and 592 km^2 of suitable habitat for red pandas in Nepal, respectively. These estimated suitability variations may be due to differences in the methodology and incorporated variables. Previous studies used fir forest cover, elevation range, and key informant information to estimate the habitat; however, recent studies have used species occurrence records, climate and topographic features in statistical models. Our model clearly predicted the habitat as including the Rasuwa, Nuwakot, Myagdi, Baglung and Dhading districts in central Nepal, which include the recently described red panda distribution from a national survey (Bista et al., 2017).

4.2. Sign distribution with respect to elevation, substrate, aspect and forest type

Evidence of red panda feces was encountered between 2400 and 3800 m, with an average of 3200 m (3200 $\pm$ 300 m), in the field; however, the eastern region showed an average elevation range below 3000 m, indicating a distribution at a lower elevation compared to those of the other study areas. Similarly, Thapa et al. (2018) observed an average elevation range above 3000 m in Nepal along with other countries, including India and Bhutan, but an average below 3000 m in China and Myanmar. The records of the elevation range were similar to previous studies by Bhatta et al. (2014) in Jumla, Sharma et al. (2014) in RNP, Panthi et al. (2012) in DHR, Bista et al. (2017) in central Nepal, Yonzon and Hunter (1991) in LNP, Thapa and Basent (2015) in LNP, Thapa et al. (2014) in GCA and Williams (2003) in Ilam. Fallen logs, the forest floor, tree branches and rock were observed to be the predominant substrates for defecation, which were almost similar in proportion except for rock. Bista et al. (2017) determined that tree branches were the most common defection substrate and that the least common was rock. Bhatta et al. (2014) reported that the red panda predominantly used fallen logs as defection locations but used rock the least, which is supported by our study. However, our study showed a similar percentage of sign records on all three substrates. In the field observations, slightly inclined logs ($\leq 45°$) that had fallen on another tree provided the preferred defecation locations because the logs provided a suitable position for grasping bamboo leaves and a safe place from predators. The defecation substrate differs seasonally (Williams, 2003) with the requirement of nutritious food, e.g., during the growth season of bamboo shoots, defecations occurred on the forest floor. Prior studies have suggested that fallen logs are an important habitat component for the red panda (Wei et al., 2000; Pradhan et al., 2001) and could benefit the foraging strategy of this species.

Aspect and forest types are important habitat features to build habitat suitability for the red panda (Thapa et al., 2018). A high percentage of sign occurrence was observed in the northern aspect (north, northwest, northeast), mainly in the northeast. Similar observations were reported in central Nepal, indicating that the northeast aspect is the most preferred (Yonzon, 1989; Bista et al., 2017), which provides better climatic conditions for the growth of bamboo. The northern aspect has more moisture with greater canopy cover than the southern aspect; these two factors both have a positive influence on vegetation growth, including bamboo species. The varied climate and steepness of the topography influence the vegetation composition and cause aspect preference differences of red pandas while moving from the eastern to the western part of the country. In the field observations, the high bamboo coverage in the northern (north, northeast) aspects is associated with the availability of additional food along berries plants, and water sources and exposure of sunlight. During winter, there is snow covered in the habitat of red panda in the Himalayas. Additionally, delayed snow melt in the northern aspects delays plant maturation and leads to higher forage quality compared to southern aspects later in the season (Hay and Heide, 1984).

The occurrence of red panda signs was recorded in ten different forest types across Nepal, and showed significant differences among forest types. The forest types observed in the eastern region were distinct from those in western Nepal, with the exception of fir forest, which is a common forest type throughout the country and was identified as a major habitat. The large occurrences of red panda signs encountered within fir forest justify it as a preferred red panda habitat in Nepal. Similarly, fir forest is the most preferred habitat of the Himalayan musk deer, which inhabit the same elevation ranges (Aryal et al., 2010; Singh et al., 2018). Apart from fir forest, other important forest types were mixed broadleaf forest and East Himalayan oak-laurel forest in eastern Nepal; temperate mountain oak forest in central Nepal and temperate juniper forest and blue pine-spruce forest in western Nepal. These classified forest types were based on the location of red panda occurrence and data from an ecological vegetation database adopted by (Thapa et al., 2016). Most previous studies have classified forests based on dominant tree species in sign plots, which limits the description of different forest types.

4.3. Influencing environmental group covariates

Species habitat association was governed by the interactive actions of multiple environmental factors in a multidimensional space. However, the degree of influence depends on key variables and the spatial scale. The distribution range of the red panda was a narrow altitudinal band (2400−3800 m) in different forest types from eastern to western Nepal. The distribution was expected to be influenced by the combined effects of habitat features, geography, spatial climate variables, and anthropogenic disturbances on a broad scale. Multiple factor analysis confirmed the existence of the main variable gradient and the validity of splitting this gradient into four categories: habitat, geography, climate and disturbance. This study indicated that the habitat, geographic and climate groups of covariates best explained the occurrence of the red panda on a broad scale.

Habitat, geography and climate were important groups for determining the habitat association and occurrence status of the red panda in the Himalayas. Disturbance had a very low influence compared to the other factors. The dimensions (1−5) of MFA showed that habitat and geography had more important roles than the spatial climate variables. Both the habitat and geographic groups consisted of a wide range of variables, including the forest type, canopy cover, bamboo cover, fallen logs, elevation, aspect, slope and others. Previous studies have concluded that all of these variables are important attributes for performing macro and microhabitat analyses of the red panda (Yonzon, 1989; Wei et al., 2000; Pradhan et al., 2001a,b; Thapa et al., 2018). The habitat in the area is varied, and the conditions rely on environmental factors, including the topography and climate, which have a significant influence on animal survival and distribution (Pradhan et al., 2001; Zhang et al., 2008). Habitat features are expected to be better predictors of animal distribution than topography and climate at local scales. Other studies have shown that at the local scale, the structural complexity of the habitat is more important than the vegetation composition for the occurrence of mammalian species in remnant habitat fragments in urban areas (Garden et al., 2007). This study found a geographic variable group that consists of slope, aspect, elevation and distance proximity, i.e., the distance to rivers, roads and settlements that contributes to red panda detection. Slope and aspect have an indirect role in balancing the vegetation composition by altering the temperature and amount of rainfall. The red panda habitat would have been influenced by the slope and aspect because the vegetation composition of Himalayan tree line ecotones varies greatly depending on the slope and aspect (Schickhoff et al., 2014) and because red pandas inhabit tree line ecotones in the Himalayas. Furthermore, the red panda prefers steeper slopes farther away from settlements (Wei et al., 2000).

Red panda occurrence was positively associated with spatial climate variables. These climatic variables are used in species distribution modelling to predict past, current and future potential habitats of a study species (Hijmans et al., 2005). In this study, climatic variables were incorporated as a separate group of variables in MFA and had a high positive contribution in all five dimensions. In addition, logistic regression models showed a significant relationship with the records of sign presence of the red panda. Climate associated variables are typically considered to be the most important determinant of species occurrence (Pearson and Dawson, 2003). Similarly, climate plays an important role in determining species' distribution and evaluating the influence of environmental variables (Morelle and Lejeune, 2015) when modeled as covering a large geographical area. Kandel et al. (2015) showed climatic influences on red panda occurrence, which might be due to the coverage of a large geographic area, and found a similar result as we found in this study. Temperature and precipitation have been shown to greatly influence the growth rates of bamboo species understories, which constitute more than 90% of the red panda diet.

4.4. Influence of key specific covariates

This study revealed that red panda occurrence was associated with forest type, canopy cover, substrate use and bamboo cover, which were included as habitat variable groups in MFA. These variables had a considerable influence on the macro and microhabitat of the red panda. The individual variable contribution in MFA showed that the forest types of mixed broadleaf forest and East Himalayan oak-laurel forest had a high contribution in the habitat association of the red panda, greater than other forest types, although other types were also positively associated. In addition, most red panda occurrences were recorded in fir forests, a common forest type throughout the study sites. P. B. Yonzon et al., 1991; P. Yonzon et al., 1991 incorporated fir forest into the habitat suitability model of the red panda. Red panda occurrences were confined to cool broadleaf and coniferous forests in Bhutan but were strongly associated with old growth Bhutan Fir on a fine scale (Dorji et al., 2012). However, Yonzon and Hunter (1991) and Pradhan et al., 2001a, 2001b reported that coniferous forest was the second major forest type preferred by the red panda, next to mixed coniferous forest. Similarly, Ghose et al. (2011) suggested that mixed coniferous and oak forests were suitable red panda habitats in protected areas of Sikkim state. One plausible reason for the preference of oak forest could be the potential availability of oak trees with large trunks for building dens during breeding season. Due to variations in climate and topography across the entire range, the red panda habitat consists of different vegetation compositions, including evergreen forests, evergreen and deciduous mixed broadleaf forests, deciduous forests, deciduous and coniferous mixed forests, and coniferous forests with associated bamboo thicket understories (Yonzon et al., 1991a; Wei et al., 1999).

Other variables (canopy cover, substrate use, bamboo cover, grazing, tree stumps and fallen logs) were associated with the red panda habitat. Zhang et al. (2006) suggested that slope, aspect, bamboo height, tree size, fallen logs, and tree stumps are important variables in microhabitat analysis of the red panda as well as the sympatric giant panda (Wei et al., 2000; Kang et al., 2013). Similarly, red panda occurred on steeper slopes with a higher density of fallen logs and shrubs and higher canopy and bamboo cover and also close to fallen logs, shrubs, and tree stumps (Wei et al., 2000; Zhang et al., 2004; Dorji et al., 2011). A canopy cover below 60%, with preferred coverage below 20%, was important for red panda occurrence in this study. Most studies mention that the red panda prefers high canopy cover, but these findings vary among studies; these differences may be due to specific study locations and variety of canopy classes.

The ground or forest floor (including feces on top of snow in winter), tree branches, fallen logs, and rock are substrates used by red panda for defection. MFA showed that the ground was an important defecation location. Season, tree species, tree inclination, availability of fallen logs, bamboo height, and growth of bamboo shoots could influence substrate use. Less than 20% bamboo cover was deemed as important in this study, but previous studies have suggested that dense bamboo cover is a priority. Sparely distributed bamboo cover is an important feature that could help facilitate escape from predators.

Among small, large and mixed tree fallen logs, red panda occurrence is greatly influenced by the fallen logs of small trees. Small tree fallen logs can be used as defection locations because they provide easy access to bamboo during feeding and act as walkways (Reid et al., 1991; Wei et al., 1995). This study showed that the red panda preferred areas without grazing activity. There is no direct competition between livestock and the red panda for food resources (Yonzon, 1989), but grazing activity could affect habitat degradation through trampling. Sharma et al. (2014) noted that red panda occurrence was affected by livestock grazing in Rara National Park. Field observations suggested that there is coexistence of the red panda and livestock in the Himalayas. However, livestock-guarding dogs would affect this coexistence. Furthermore, livestock grazing seasons in transhumant pastoral systems and the birth of red panda cubs overlap in these areas. The parental care behavior of the red panda could be disturbed by herders, guard dogs, and livestock grazing. Similarly, Yonzon (1989) concluded that high infant mortality in wild red pandas was due to human activities in the panda habitat.

In the quantitative group of climate and geography, elevation made a significant contribution to determining red panda occurrence. Other variables, such as the distance to settlements (away from settlements), distance to roads (away from roads), annual temperature range (bio7), mean diurnal range (bio 2), and annual precipitation (bio12), were attributed to red panda occurrences. Similarly, elevation is a strong predictor of red panda distribution in Nepal (Mahato, 2010). However, Kandel et al. (2015) considered climate to be a better predictor than elevation in the distribution mapping of the red panda. Elevation did not directly affect the species' distribution, but was correlated with other relevant predictors, such as temperature, rainfall, and solar radiation (Elith et al., 2006a), that lead to a change in habitat features. Elevation has been included in performing distribution, habitat use and habitat suitability analyses (Yonzon et al., 1991a, Yonzon et al., 1991; Bhatta et al., 2014; Bista et al., 2017; Panthi et al., 2017). The distances from settlements and roads were important factors in the red panda habitat, and these results are also supported by a previous study (Wei et al., 1999). Similarly, the potential distribution of the red panda habitat based on spatial climate variables was a good predictive model (Mahato, 2010; Kandel et al., 2015). Temperature and rainfall contribute to the vegetation structure, particularly the growth of different bamboo species, which is a primary food of the red panda.

5. Conclusion

Understanding the influences of habitat variables and important ecological requirements of the red panda is essential for better habitat management that has enlightened through this study. The potential habitat of the red panda is distributed in a narrow elevation across the country. Such potential habitat would be highly sensitive from anthropogenic activities thus management interventions should be priorities to protect habitats. Furthermore, our study filled a gap in the ecological knowledge of habitat requirements at the microhabitat and landscape levels. Our study strongly suggests that red panda occurrence is broadly influenced by a group of variables, including habitat, climate and geography, as well as by disturbance. Mixed broadleaf forest, East Himalayan oak-laurel forest, canopy cover >20%, ground substrate use, bamboo cover >20%, tree stump presence, fallen logs of small trees and grazing absence are important variables in habitat of the red panda. Implementation of habitat management practices in consideration of these important ecological requirements will be vital for conservation of the red panda in the Nepal Himalayas.

Author contributions

Conception of the study: AT, YH, FW and field survey design: AT, PBS, FW; Fieldwork and data collection: AT; Data analysis: AT, PCA; and Writing the article: AT, YH, FW, KBS; Final edits: all authors.

Ethical standards

All required permissions for our surveys were provided by Department of National Parks and Wildlife Conservation (DNPWC), Nepal (Permission Letter no. 217/2623).

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00890.

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