



Original Research Article

Impacts of livestock grazing, topography and vegetation on distribution of wildlife in Wanglang National Nature Reserve, China



Cheng Tian^a, Pei-Chun Liao^b, Buddhi Dayananda^c, Yu-Yang Zhang^a,
Zheng-Xiao Liu^a, Jun-Qing Li^{a,*}, Bing Yu^d, Li Qing^e

^a Beijing Key Laboratory for Forest Resources and Ecosystem Processes, Beijing Forestry University, 35 Qinghua East Road, Haidian District, Beijing, 100083, China

^b School of Life Science, National Taiwan Normal University, No. 88, Sec. 4, TingChow Rd, Wunshan Dist, Taipei, 116, Taiwan

^c School of Life Sciences, University of Technology Sydney, Broadway, NSW, 2007, Australia

^d Wanglang National Nature Reserve Administration, Pingwu County, Mianyang City, Sichuan Province, 622550, China

^e Gaocun Forestry Station, Pingwu County Forestry Bureau, Pingwu County, Mianyang City, Sichuan Province, 622550, China

ARTICLE INFO

Article history:

Received 24 May 2019

Received in revised form 22 July 2019

Accepted 22 July 2019

Keywords:

Giant panda grazing livestock

Interspecific disturbance

Landscape effect

Niche partitioning

Species co-occurrence

Wanglang national nature reserve

ABSTRACT

Successful conservation requires that we identify factors affecting species co-occurrence in the wild and understanding the consequence for wildlife management. We investigated species diversity in Wanglang National Nature Reserve using camera traps. We conducted vegetation surveys and obtained topographic information at each camera trapping site. We determined the characteristic species of trees and wildlife at each site using PCA. Generalized Linear Models of the effect of landscape structure (including the terrain and vegetation) and co-occurrence of wildlife species on occurrence of characteristic species were compared. Model selection showed that the global model out-performed all other models. The effect of species co-occurrence explained the most variation in species occurrence, while terrain and dominant tree species also had explained a high proportion. The co-occurrence of wildlife is affected by the distribution of terrain-dependent vegetation and dominant tree species, especially in the case of arboreal animals, which implies a high degree of niche partitioning. In contrast, terrestrial animals are more affected by species co-occurrence. Obvious mutual exclusivity is shown between grazing livestock (e.g. the cattle) and medium-to-large mammals such as giant panda and tufted deer. This may be attributed to the complete niche differentiation between these species, and indicates the effects of anthropogenic activities on wildlife in the reserve. These results indicate that the maintenance of a complex landscape is helpful for maintaining diverse resources and niches for wildlife. Reducing or adequately managing grazing activity is urgent for protecting medium- and large-sized mammals in the reserve.

© 2019 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

* Corresponding author.

E-mail address: lijq@bjfu.edu.cn (J.-Q. Li).

1. Introduction

Environmental factors, such as topographical features, soil properties, and water and light intensity are the main factors affecting species composition of communities (Li et al., 2011, 2017; Sharpe and Baldwin, 2013; Sellan et al., 2019). Integrated effects of climate change and human disturbances on vegetation succession and ecosystem function have also impacted wildlife diversity (Mitchell et al., 2014; Ashton et al., 2015). For example, climate change is a potential threat to giant pandas (*Ailuropoda melanoleuca*) and their habitats (Zang et al., 2017). Anthropogenic activity such as deforestation, poaching, and livestock grazing, have led to dramatic decline of global and local biodiversity (Sala et al., 2000; Zhao et al., 2007; Kang et al., 2011; Hull et al., 2014; Tilman et al., 2017; Kühl et al., 2019). Overuse of natural resources will lead to ecological imbalance, reduce biodiversity and impact conservation effectiveness (Mckee et al., 2004; Tang, 2005).

The factors affecting wildlife activities are complex. A recent study found that slope, abundance of food resources (bamboos), and distributions of large trees are the main determinants for rest sites choice of giant panda (Kang et al., 2017). The authors also emphasized the importance of terrain and resource distribution on wildlife activity. In addition, vegetation, which functions both as a food resource and as a shelter, and interspecific competition among wildlife will also affect wildlife behaviour and distribution. A recent study from China's Baishuijiang National Nature Reserve indicated that giant panda abundance was correlated with that of Chinese serow (*Capricornis milneedwardsii*) and Temminck's tragopan (*Tragopan temminckii*), but was less related to Chinese goral (*Naemorhedus griseus*) (Rong et al., 2019). This shows that revealing interspecific interactions is also important for understanding species diversity.

The camera trap is a non-invasive sampling technique used to study the occurrence of wildlife (Carver et al., 2011; Li et al., 2014). They can provide long-term and uninterrupted sample data (Nakashima et al., 2018). The species occurrence records (SOR) could reflect the magnitude of wildlife movements (Stewart et al., 2018). Examining the effect of landscape structure on species occurrence records (SOR) will improve our understanding of the use of space by wildlife. Estimating the relative abundance and density of wildlife populations, as well as analyzing the rhythm of species activity, provides important information for conservation management (Tobler et al., 2013; Alexander et al., 2016; Tian et al., 2018).

Interactions between terrain, vegetation, and co-occurring animal species on wildlife activity are particularly rarely understudied in Asia. In this study, we attempt to find the key factors determining the co-occurrence of wildlife in the Wanglang National Nature Reserve (WLNR), Sichuan Province, China. WLNR is one of the oldest nature reserves in China, and is home to many rare species (e.g. giant panda, Chinese serow, Asiatic black bear (*Ursus thibetanus*), leopard cat (*Prionailurus bengalensis*), Sichuan takin (*Budorcas tibetanus*), golden snub-nosed monkey (*Rhinopithecus roxellana*), blood pheasant (*Ithaginis cruentus*), Temminck's tragopan, etc.). The undulating terrain and complex vegetation harbors abundant wildlife.

In this study, we asked the following questions: (1) what is the key factor affecting the spatial distribution of trees? Is it the geographic factor (longitude, latitude, altitude, slope, aspect) or associated tree species? (2) What is the key determinant of the occurrence of wildlife in WLNR? Is it the geographic effects, vegetation effects, or interspecific interactions? (3) Has livestock grazing affected wildlife diversity?

2. Materials and methods

2.1. Study site

The Wanglang National Nature Reserve was established in 1965. It is located in the northern part of the Minshan Mountains, and has a total area of 32,297 hm² (Zhao, 2013). The altitude ranges from between 2300 and 4980 m above sea level. According to the climate records since 1960 to 1990 available from WorldClim (<http://www.worldclim.org/bioclim>), the annual mean precipitation and the annual mean temperature of thirty-three study sites was 752.8 mm (range from 730.3 to 779.6 mm) and 5.24 °C (range from 3.80 to 6.48 °C), respectively (Table S1). It is a global biodiversity hotspot (Myers et al., 2000) and contains abundant wildlife, including about 28 wild giant pandas (Kang et al., 2017).

2.2. Sample survey and camera trap monitoring

Thirty-three study sites were selected between 2640 and 3204 m above sea level according to topography and the characteristics of the forests (Fig. 1 and Table S1). The distance between two sites was not less than 100 m. A landscape survey was conducted in each site using a 20 m × 20 m quadrat. From this quadrat we collected geographic data (the latitude, longitude, altitude, slope, and aspect) and vegetation data (tree composition and canopy density, shrub coverage and herb coverage, bamboo coverage, and proportion of young bamboo).

An infrared automatic camera (Ltl AcornTM 6210) was set at each study site from July 2017 to May 2018. The camera location was selected based on the presence of paths with animal signs, and the camera was fixed on a tree or bamboo bush 30–80 cm away from the ground to give a relatively wide field of view, and then adjusted the lens to the right angle. The shortest distance between any two cameras was kept above 100 m to ensure the independence of the photos captured (Hu, 2013; Li et al., 2016). We were not able to identify individuals from our camera data. To avoid the duplication of records, we counted one capture of a species within 30 min as an independent event (Ohashi et al., 2014; Li et al., 2016; Gray, 2018).

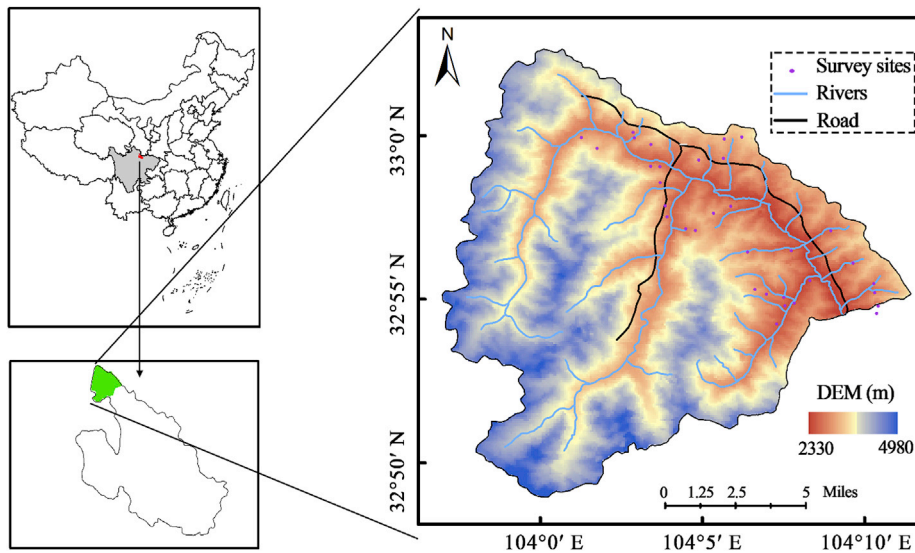


Fig. 1. The location of sampling locations and camera traps in Wanglang National Nature Reserve, Pingwu County, Sichuan Province, China.

2.3. Factors affecting the composition of forest tree species

In order to describe the tree species composition of forest community, the data matrix of relative species abundance (RA) in the study sites was converted to the linearly uncorrected variables using the principal component analysis (PCA). To simplify the data matrix of transformed linearly uncorrected variables (i.e. principal components, PCs), the first three PCs (i.e. PC1–PC3) were retained to represent the tree composition of this forest. Four species with higher eigenvalues in the eigenspace formed by the first and second axes with the highest interpretability were designed as representative tree species of the forest. Representative species denote the species that can best represent the group of species within a community and the habitats they associate with. A generalized linear model (GLM) was then used to verify whether the geographic effect and the associated tree species affect the RAs of each representative tree species, in which the RAs of four representative tree species were set as the responses and the position (longitude and latitude) and vertical (altitude) spatial distribution, terrain (aspect and slope), and the associated tree species (PC1–PC3 of tree species) were set as predictors. A hierarchical model test was conducted to test the horizontal spatial effect, geographic (horizontal + terrain) effect, and full model (geographic + tree-species associated trees) in GLM using a likelihood ratio test (LRT).

We further performed distance-based redundancy analysis (dbRDA) to estimate the explanatory proportion of these factors on the forest composition in 999 permutations by package *vegan* in R. Data matrix of RA of trees was transformed into a Bray-Curtis distance matrix for dbRDA. Longitude, latitude, altitude, aspect, and slope were set as geographic predictors, and the first three PCs of trees were set as the associated-tree factors. The *post hoc* type-II ANOVA was conducted to test the significance of each explanatory variables.

2.4. Factors affecting species occurrence

To understand the situation of wildlife activity in the sample area, we set up automatic cameras to record species occurrence. In addition to comparing and analyzing the total number of wildlife occurrences in each sample area, the accumulated occurrence records were binned monthly because the activity time of each wildlife species is non-uniformly dispersed through time. The annual and monthly records are defined as the Annual Species Occurrence Records (ASOR) and Monthly Species Occurrence Records (MSOR), respectively.

We used PCA to describe the distribution of ASOR and identified the representative wildlife species in each site. Model selection was performed using LRT to find the best GLM model to predict the ASOR in the same manner as described above. Geographic factors, vegetation factors, and co-occurring wildlife (PC1–PC3 of ASOR) were set as predictors. Additionally, for considering the time of wildlife activities, we performed dbRDA to examine the proportion of explanatory variations of MSOR were explained by geographic, temporal (month), and vegetation effects and the co-occurred wildlife. Bray-Curtis distance was used to transform the MSOR data matrix and 999 permutations were conducted in dbRDA. We selected forest density, first three principal components of forest composition, herbaceous and shrub coverages, bamboo density, and proportion of bamboo seedlings in the representative indices of vegetative effect. The longitude, latitude, altitude, aspect, and slope were chosen to represent the geographic effect. The significance of each explanatory variable was tested by a *post hoc* type-II ANOVA.

Cattle is livestock occurring as a kind of grazing disturbance, which is one of the seven representative species inferred by high explanatory loadings in PCA (see results). To understand whether cattle activities promote or interfere with other wildlife, linear regressions were conducted between occurrence records of cattle and all wildlife and between cattle and the other six representative species. The effect of cattle activities was also examined to the occurrence of giant pandas, the umbrella species of this Nature Reserve. All of the analyses were conducted in R.

3. Results

3.1. Representative species in the nature reserve

We recorded 20 species of trees, belonging to 9 orders and 11 families. 48 species of animal were captured, including 20 mammals and 28 birds. They belong to 10 orders and 23 families. The PCA results show that the first three PCs explained 69.24% of the variation in forest tree composition. *Acer longipes*, *Abies faxoniana*, *Betula albo-sinensis*, and *Betula platyphylla* had relatively high loadings on the first three PCs and were considered representative of forest tree composition (Fig. 2a). The first three PCs of the ASOR data explained 71.44% of the variation in wildlife presence. Seven animal species (*Elaphodus cephalophus*, *Ithaginis cruentus*, *Zoothera dauma*, *Garrulax elliotii*, *Tamias swinhoei*, *Tarsiger indicus*, and *Bos taurus*) revealing high explanatory loadings were regarded as representative species (Fig. 2b).

3.2. Factors affecting tree species composition

Null models and single-factor models were rejected by the full models for explaining the RA of all four species. This shows that the best predictions will be obtained by considering all factors (i.e. spatial distribution, terrain, and associated trees, Table 1). In the full model GLM, the PCs of trees had a significant effect on the RA of all four representative trees (Table 2). Slope was found to significantly affects *Ac. longipes*, *Ab. faxoniana*, and *B. platyphylla*, while altitude significantly predicted the RAs of *Ac. longipes*, *Ab. faxoniana*, and *B. albo-sinensis* (Table 2). The results of model selection and GLM were verified by the dbRDA: all factors significantly contribute to explaining variation in RA of tree species (Table 3). Among the factors, tree species (tree PC1~3) accounted for 46.7% of variation explained, slope accounted for 10.2%, and elevation accounted for 7.6% (Table 3). These results show that horizontal spatial distribution has a low impact on forest species composition, while terrain and associated tree species have a significant and decisive impact on tree species composition.

3.3. Factors affecting wildlife occurrence

The null model could not be rejected by any model describing single or various combinations of geographical factors and tree species compositions (Table 4). Only when full models are added did null models and other simpler models perform comparatively poorly (Table 4). This result indicates that wildlife interaction plays an important role in species presence. This is verified by the summary statistic of the full-model GLM, which shows significant effect of ASOR PC1 and PC2 on wildlife activities in all representative animals, and of ASOR PC3 on four species (*I. cruentus*, *G. elliotii*, *T. swinhoei*, *B. taurus*) (Table 5). Tree PC2 also had a significant effect on four wildlife species (*Z. dauma*, *G. elliotii*, *Tar. indicus*, and *B. taurus*), indicating the effect of tree community composition on wildlife. For the MSOR of all wildlife, all constraint factors significantly explain 37.1% of variation in wildlife occurrence patterns. Wildlife PC1~PC3 explained 21.9% variation in MSOR, while tree PC2 explained 1.1% (Table 6). The result of dbRDA is in agreement with the speculation that the species co-occurrence is crucial to wildlife

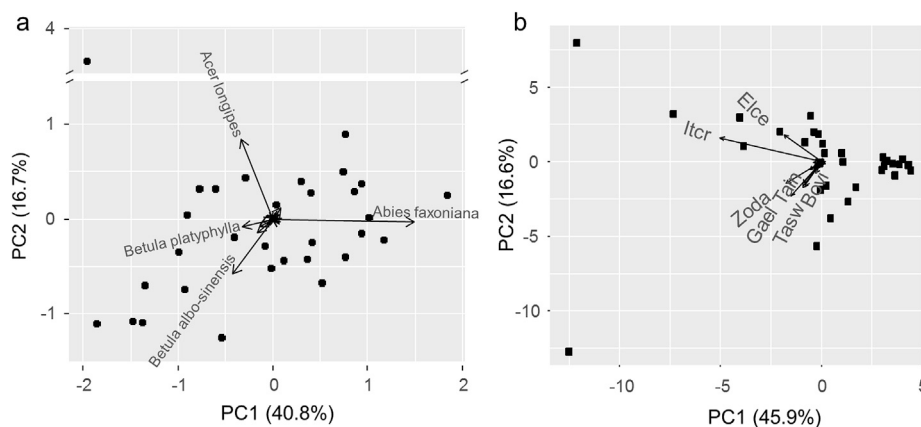


Fig. 2. Principal component analysis (PCA) revealing (a) tree species composition and (b) wildlife composition in Wanglang National Nature Reserve. Arrow lengths indicate loadings of explanatory variables.

Table 1

Results of model selection of GLMs for testing the effect of geographic variables and associated-tree-species on the relative abundance of four representative forest trees.

Null vs. Alternative	df	<i>Acer longipes</i>		<i>Abies faxoniana</i>		<i>Betula albo-sinensis</i>		<i>Betula platyphylla</i>	
		Dev	P	Dev	P	Dev	P	Dev	P
Model 1 vs. Model 2	2	0.035	1.89e-8*	0.043	3.41e-14*	0.009	0.113	0.043	0.003*
Model 1 vs. Model 3	3	0.161	0.140	0.063	0.8521	0.065	5.41e-7*	0.046	0.542
Model 2 vs. Model 3	1	0.126	< 2.2e-16*	0.020	7.03e-8*	0.056	1.52e-7*	0.003	0.363
Model 2 vs. Model 4	3	0.192	0.086	1.083	2.26e-5*	0.260	3.27e-3*	0.034	0.026*
Model 3 vs. Model 4	2	0.066	2.72e-15*	1.063	< 2.2e-16*	0.204	< 2.2e-16*	0.031	0.015*
Model 4 vs. Model 5	3	0.734	< 2.2e-16*	1.148	< 2.2e-16*	0.444	< 2.2e-16*	0.485	< 2.2e-16*

Model 1 (empty model): ~1.

Model 2 (horizontal spatial distribution): ~ Longitude + Latitude.

Model 3 (horizontal and vertical spatial distribution): ~ Longitude + Latitude + Altitude.

Model 4 (spatial distribution and terrain): ~ Longitude + Latitude + Altitude + Aspect + Slope.

Model 5 (full model): ~ Longitude + Latitude + Altitude + Aspect + Slope + Tree.PC1 + Tree.PC2 + Tree.PC3.

*P < 0.05.

Table 2

Results of the GLM modelling effects of geographic variables and associated-tree-species on the relative abundances of four representative forest trees.

	<i>Acer longipes</i>		<i>Abies faxoniana</i>		<i>Betula albo-sinensis</i>		<i>Betula platyphylla</i>	
	t	P	t	P	t	P	t	P
Intercept	-0.832	0.414	-0.256	0.800	-2.038	0.053	-0.244	0.809
Longitude	0.761	0.455	0.170	0.866	1.861	0.076	0.062	0.951
Latitude	0.905	0.375	0.458	0.651	2.168	0.041*	0.580	0.568
Altitude	-3.851	0.001*	-2.967	0.007*	-4.525	1.52e-4*	-1.708	0.101
Aspect	-0.401	0.692	-0.527	0.604	0.031	0.976	-0.796	0.434
Slope	2.948	0.007*	3.187	0.004*	1.513	0.144	2.612	0.016*
Tree PC1	-9.255	3.23e-9*	39.939	< 2e-16*	-7.474	1.35e-7*	-5.115	3.51e-5*
Tree PC2	23.575	< 2e-16*	-0.803	0.430	-11.837	2.90e-11*	-0.740	0.467
Tree PC3	-7.786	6.81e-8*	-2.718	0.012*	-7.071	3.33e-7*	9.768	1.19e-9*

*P < 0.05.

Table 3

Results of the distance-based redundancy analysis (dbRDA) for vegetation types.

	S.S.	Proportion	F	P
Total	6.636	1.000		
Constrained	5.222	0.787		
Longitude	0.194	0.029	3.151	0.013*
Latitude	0.163	0.025	2.653	0.039*
Altitude	0.507	0.076	8.244	0.001*
Aspect	0.583	0.088	9.478	0.001*
Slope	0.675	0.102	10.981	0.001*
Tree PC1	0.843	0.127	13.714	0.001*
Tree PC2	1.433	0.216	23.312	0.001*
Tree PC3	0.824	0.124	13.406	0.001*
Residual	1.414			

*P < 0.05.

activities. Particularly noteworthy is the impact of time. Time effect is small but significant (0.7% explanatory variation, $P = 0.008$), suggesting that although species occurrence is time-affected, the amplitude of impact is still less than that of topography (1.0%, 1.5%, and 1.4% for altitude, aspect, and slope), vegetation (8.7%) and the co-occurring species (21.9%) (Table 6).

We found that despite slight fluctuations in the ASOR in regions with low shrub and herbaceous coverage, shrubs and herbaceous vegetation do not significantly affect the ASOR, unlike trees and bamboos. The frequency of occurrence of most species increased when there were >10 trees per quadrat (20 m × 20 m), but did not continue to increase with tree abundance, reaching a downward trend at > 15 trees per quadrat, with the exception of *T. swinhoi* (Fig. S1). The terrestrial bird *I. cruentus* favors environments with a slight slope and high tree species richness. Giant panda tends to occur in relatively flat environments, with slightly lower tree species richness (richness = 2) and abundance (8–9 trees per quadrat), and higher bamboo density and young bamboo abundance. Interestingly, other wildlife (except *E. cephalophus*) tended to occur in regions with poor bamboo regeneration rate, i.e. low abundance of young bamboos (Fig. S1). This shows that most animals and giant pandas occupy different niches with regards food resources and space utilization.

Table 4

Model selection for the best fit GLM for testing the effect of geographic variables and associated-tree-species on the relative abundances of four representative forest trees.

Null vs. Alternative	df	<i>Elaphodus cephalophus</i>		<i>Ithaginis cruentus</i>		<i>Zoothera dauma</i>		<i>Garrulax elliotii</i>		<i>Tamiops swinhoei</i>		<i>Tarsiger indicus</i>		<i>Bos taurus</i>	
		Dev	P	Dev	P	Dev	P	Dev	P	Dev	P	Dev	P	Dev	P
Model 1 vs. Model 2	2	116.170	0.461	7.702	0.984	30.204	0.765	116.530	0.334	73.523	0.522	37.063	0.411	23.528	0.695
Model 1 vs. Model 3	3	116.800	0.682	59.084	0.970	32.007	0.908	137.540	0.469	128.240	0.520	60.958	0.401	28.865	0.833
Model 2 vs. Model 3	3	0.627	0.929	51.382	0.645	1.803	0.861	21.016	0.534	54.718	0.326	23.895	0.283	5.337	0.689
Model 1 vs. Model 5	4	161.310	0.854	564.600	0.800	121.020	0.844	163.410	0.724	247.890	0.494	63.884	0.719	33.848	0.966
Model 2 vs. Model 3	4	45.144	0.908	556.900	0.510	90.815	0.676	46.880	0.846	174.370	0.378	26.821	0.751	10.319	0.962
Model 3 vs. Model 2	4	44.517	0.762	505.520	0.350	89.012	0.473	25.864	0.799	119.650	0.346	2.926	0.936	4.983	0.932
Model 1 vs. Model 8	5	224.410	0.962	818.640	0.926	644.820	0.069	289.180	0.772	423.630	0.479	77.145	0.925	113.520	0.929
Model 2 vs. Model 6	5	108.240	0.977	810.940	0.796	614.620	0.031	172.660	0.821	350.110	0.397	40.082	0.950	89.990	0.874
Model 3 vs. Model 5	5	107.620	0.945	759.560	0.714	612.820	0.017	151.640	0.769	295.390	0.385	16.187	0.985	84.654	0.806
Model 4 vs. Model 3	5	63.099	0.873	254.040	0.808	523.810	0.008	125.780	0.549	175.740	0.372	13.261	0.910	79.671	0.539
Model 1 vs. Model 11	6	1630.00	9.09e-7	6680.80	< 2.2e-16	1452.10	< 2.2e-16	1496.00	< 2.2e-16	1523.70	< 2.2e-16	561.22	< 2.2e-16	823.94	< 2.2e-16
Model 2 vs. Model 9	6	1513.80	7.15e-7	6673.10	< 2.2e-16	1421.90	< 2.2e-16	1379.50	< 2.2e-16	1450.20	< 2.2e-16	524.15	< 2.2e-16	800.41	< 2.2e-16
Model 3 vs. Model 8	6	1513.20	2.86e-7	6621.70	< 2.2e-16	1420.00	< 2.2e-16	1358.50	< 2.2e-16	1395.50	< 2.2e-16	500.26	< 2.2e-16	795.07	< 2.2e-16
Model 4 vs. Model 6	6	1468.70	6.63e-8	6116.20	< 2.2e-16	1331.00	< 2.2e-16	1332.60	< 2.2e-16	1275.80	< 2.2e-16	497.33	< 2.2e-16	790.09	< 2.2e-16
Model 5 vs. Model 3	6	1405.60	3.40e-9	5862.10	< 2.2e-16	807.24	2.64E-16	1206.80	< 2.2e-16	1100.10	< 2.2e-16	484.07	< 2.2e-16	710.42	< 2.2e-16

Model 1 (empty model): ~1.

Model 2 (horizontal spatial distribution): ~ Longitude + Latitude.

Model 3 (horizontal and vertical spatial distribution): ~ Longitude + Latitude + Altitude.

Model 4 (spatial distribution and terrain): ~ Longitude + Latitude + Altitude + Aspect + Slope.

Model 5 (geographic and forest tree effect): ~ Longitude + Latitude + Altitude + Aspect + Slope + Tree.PC1 + Tree.PC2 + Tree.PC3.

Model 6 (full model): ~ Longitude + Latitude + Altitude + Aspect + Slope + Tree.PC1 + Tree.PC2 + Tree.PC3 + ASOR.PC1 + ASOR.PC2 + ASOR.PC3.

Table 5

Summary results of the GLM revealing effect of geographic variables, tree species composition, and co-occurrence of wildlife on the occurrence records of seven representative wildlife species.

	<i>Elaphodus cephalophus</i>		<i>Ithaginis cruentus</i>		<i>Zoothera dauma</i>		<i>Garrulax elliotii</i>		<i>Tamiops swinhoei</i>		<i>Tarsiger indicus</i>		<i>Bos taurus</i>	
	t	P	t	P	t	P	t	P	t	P	t	P	t	P
Intercept	0.710	0.486	-0.560	0.582	-1.000	0.329	1.232	0.232	-0.466	0.646	1.138	0.269	-0.260	0.797
Longitude	-0.966	0.346	0.800	0.433	0.842	0.410	-1.460	0.160	0.374	0.712	-0.952	0.352	0.227	0.823
Latitude	-0.118	0.907	0.034	0.973	1.169	0.256	-0.640	0.529	0.601	0.554	-1.354	0.191	0.298	0.769
Altitude	-0.678	0.506	0.617	0.544	0.416	0.682	0.410	0.686	-1.284	0.214	0.985	0.336	-0.482	0.635
Aspect	-0.192	0.849	0.361	0.722	-1.027	0.317	0.737	0.470	-0.414	0.684	0.000	1.000	0.086	0.932
Slope	0.930	0.363	-0.908	0.375	-0.395	0.697	0.350	0.730	0.496	0.625	-0.159	0.875	-0.782	0.444
Tree PC1	-0.200	0.843	0.175	0.863	-0.857	0.402	0.906	0.376	-0.752	0.461	0.969	0.344	1.085	0.291
Tree PC2	-0.995	0.332	0.638	0.531	3.408	0.003*	-2.165	0.043*	2.086	0.050†	-2.733	0.013*	-4.581	1.81e-4*
Tree PC3	0.374	0.712	-0.284	0.780	-0.827	0.418	0.630	0.536	-0.898	0.380	1.869	0.076†	0.800	0.433
ASOR PC1	-5.056	6.04e-5*	-27.301	< 2e-16*	-7.708	2.06e-7*	-7.855	1.54e-7*	-4.022	0.001*	-6.754	1.43e-6*	-5.325	3.27e-5*
ASOR PC2	3.438	0.003*	6.482	2.55e-6*	-4.071	0.001*	-9.406	8.77e-9*	-4.667	1.48e-4*	-8.748	2.85e-8*	-8.747	2.86e-8*
ASOR PC3	-1.757	0.094†	2.642	0.016*	-1.019	0.320	-2.285	0.033*	7.671	2.21e-7*	-1.995	0.060†	-2.553	0.019*

*, significant ($P < 0.05$); †, marginal significant ($0.05 < P < 0.10$).

3.4. Impact of grazing

Domesticated cattle (*B. taurus*) were one of the representative animals (Fig. 2b). Cattle ASOR is positively correlated with the ASOR of all wildlife ($t = 4.726$, $P = 4.70e-5$). Among six other representative animals, we found that there was a significant

Table 6

Results of the distance-based redundancy analysis (dbRDA) showing the explanatory proportion of independent variables and the significance of explanation on the occurrence records (MSOR) of wildlife in Wanglang National Nature Reserve.

	S.S.	Proportion	F	P
Total	122.790	1.000		
Constrained	45.57	0.371		
Longitude	1.580	0.013	4.787	0.001*
Latitude	0.774	0.006	2.345	0.014*
Altitude	1.178	0.010	3.571	0.001*
Aspect	1.801	0.015	5.458	0.001*
Slope	1.729	0.014	5.240	0.001*
Month	0.820	0.007	2.484	0.008*
Tree density	1.171	0.010	3.548	0.001*
Herbaceous coverage (%)	0.798	0.006	2.417	0.012*
Shrub coverage (%)	1.450	0.012	4.395	0.001*
Bamboo density	1.209	0.010	3.662	0.001*
Young bamboo (%)	1.647	0.013	4.990	0.001*
Tree PC1	1.487	0.012	4.505	0.001*
Tree PC2	1.390	0.011	4.212	0.001*
Tree PC3	1.609	0.013	4.875	0.001*
Wildlife PC1	12.749	0.104	38.633	0.001*
Wildlife PC2	8.509	0.069	25.787	0.001*
Wildlife PC3	5.674	0.046	17.194	0.001*
Residual	77.218	0.629		

* $P < 0.05$.

positive correlation of three arboreal birds (*Z. dauma*, $t = 3.083$, $P = 0.004$; *G. elliotii*, $t = 7.662$, $P = 1.22e-8$; *Tar. indicus*, $t = 9.827$, $P = 4.86e-11$) and a marginal positive correlation of the arboreal striped squirrel (*Tam. swinhoei*, $t = 1.754$, $P = 0.089$) with cattle activities (Fig. 3). However, such significance was not found in blood pheasant (*I. cruentus*, $t = 1.512$, $P = 0.141$) and tufted deer (*E. cephalophus*, $t = 0.495$, $P = 0.624$). We also examined the activity of cattle and giant pandas, the umbrella species of the Nature Reserve, and found no significant linear relationship between the activities of these large animals ($t = -0.648$, $P = 0.522$, Fig. 3).

4. Discussion

4.1. The emergence of species determined by coexisting species may be attributed to niche partitioning

Our integrated assessment indicates that co-existing species and terrain play crucial roles in shaping patterns of species diversity in both trees or wildlife. Previous studies have mostly emphasized environmental heterogeneity on the occurrence of wildlife, especially the vegetation distribution and resource availability (Rogers and Myers, 1980; Johnson et al., 2004; Wangdi et al., 2018; Yuh et al., 2019). Some studies discussing species interactions also emphasize competition for limited resources (e.g. Dubowy, 1988; Marshal et al., 2008; Morelli and Tryjanowski, 2015). Our research points out that the frequency of species occurrence is likely to be directly affected by activities of other animals, and such species co-occurrence or exclusion is likely conducive to niche partitioning and avoiding excessive competitive pressures due (Rich et al., 2017; Weyde et al., 2018). Particularly noteworthy is the effect of such interspecific interaction on species coexistence, not only among wildlife, but also in the distribution of forest species. This suggests that niche partitioning is critical for habitat selection of forest organisms.

The inference of niche partitioning is also supported by the significant effect of time on wildlife occurrence, that is, different animals use the resources provided by forests in different seasons. Nevertheless, the regression coefficients for time were not large (0.7%, Table 6), which shows that the trend of wildlife activities in a year is still mainly affected by topographic factors. This may be because the spatial scale of this study is not large enough to reflect species migration with seasonal resource changes. However, the spatial-scale effect on the estimation of richness tends to be smaller than the density of a single species population (Gestich et al., 2019). Our estimates of species richness are therefore more reliable than estimates of abundance.

4.2. Terrain is the key abiotic factor affecting forest species diversity

Although species interactions affect co-occurrence, external factors, such as topography and vegetation, also constrain and select for occurrence of different organisms. For instance, the difference of temperature and precipitation along altitudes, the different light intensity at different aspects, and/or the selection of trees with different rootholds by the slope gradient may cause uneven spatial distribution of vegetation and wildlife. Many studies have shown that debris flows, landslides, and even earthquakes directly affect the topographic and geomorphological changes of WLNR, and thus change the local vegetation composition (Wang and Li, 2008). Previous studies have indicated that the landslides caused by earthquakes have caused

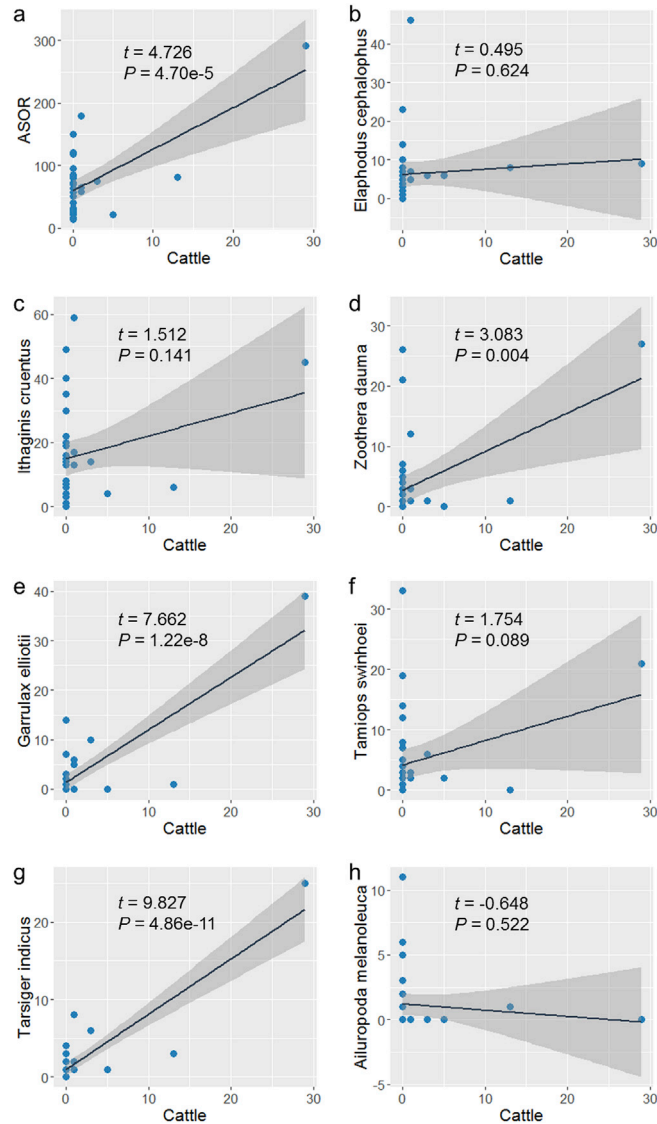


Fig. 3. Linear regressions display the positive effect of cattle interference on wildlife activities. (a) Significant influence on annual species occurrence records (ASOR); (b)–(g) cattle impact on the occurrence of six representative wildlife, in which the influence on three avian species (*Zoothera dauma* (d), *Garrulax elliotii* (e), and *Tarsiger indicus* (g)) are positively significant; (h) the influence of cattle on the occurrence of giant panda. Although the effect of cattle is non-significant, giant pandas seem to have avoided cattle activities.

severe loss of tree and shrub coverages, and that some species (e.g. giant panda) did not use habitats with low-shrub coverage and low tree and bamboo density (Wang and Li, 2008; Kang et al., 2014). Our study shows that terrain affects forest tree composition, while terrain and tree composition also affect the local-pattern and process of wildlife, e.g. species interaction, movements between patches, resource availability, etc. This not only supports the above conclusion, but also emphasizes the importance of landscape and vegetation integrity for the conservation of wildlife diversity.

4.3. Forest tree species have great influence on arboreal animals (e.g. birds)

There is an old proverb in China: A smart fowl perches only on a fine tree (which means that excellent people tend to live in a good environment). This is also true in our case. Arboreal animals are the ones that will be most affected by the species composition of tree communities (Table 5). This indicates that arboreal birds have a high degree of selectivity for micro-habitats. The tree species related to these arboreal birds are mainly the species associated with the second PC (*Ac. longipes* and *B. albo-sinensis*, Fig. 2). From the ASOR data, the eigenvectors of these arboreal animals point to similar dimensions in the PCA (Fig. 2b), indicating a similar trend of occurrence of these species throughout the year. However, the eigenvectors of the tree

species where these arboreal animals occur (i.e. *Ac. longipes* and *B. albo-sinensis*) point in the opposite direction (Fig. 2a), indicating the importance of habitat differentiation to the spatial allocation of co-occurring arboreal animals. It also highlights the importance of forest tree diversity for wildlife's habitat selection.

In addition, some sampling locations had a high species richness, while others contained very few species. These hotspots and coldspots may lead to a higher rate of false positives when investigating species co-occurrence rates. However, the preferences of most species for specific locations or environments will cause mutual interference (both positive and negative). This over-centralized space utilization driven by resource distribution and the environment may result in higher pressures for space competition or space partitioning in wildlife with a narrower range of activities. In other words, species with a limited range of activities will have higher resource niche differentiation to reduce competitive pressure, which also explains why species of forest trees have a more significant impact on the emergence of arboreal birds and squirrels, which have smaller territories than giant pandas and tufted deer.

4.4. Effects of grazing on vegetation distribution and disturbance to wildlife

The occurrence of terrestrial birds (*I. cruentus*) and tufted deer (*E. cephalopus*) that feed on shrubs or herbs is less explained by tree species composition, and only the ASOR significantly predicts their occurrence (Table 5). This result indicates that terrestrial wildlife is more susceptible to another animals' activity. Therefore, the introduction of other species (such as cattle) in the WLNR region may interfere with terrestrial wildlife. Cattle is representative of grazing disturbance intensity in the WLNR. The linear regression shows a significant positive correlation between cattle and three species of arboreal birds. Despite being arboreal, these bird species use the ground as refuge or for foraging (Dinata et al., 2008). We suspect that cattle presence may drive away the natural enemies or competitors of these arboreal birds.

It is worth noting that giant pandas are susceptible to the presence of other animals, especially cattle. When examining the data carefully, we can see that the non-significant correlations of cattle with both giant pandas and tufted deer are due to the fact that most automatic cameras that recorded cattle did not capture giant pandas or tufted deer, and *vice versa* (Fig. 3). This means that the territories of the larger species do not overlap with cattle grazing areas. These results imply that expansion of grazing activity reduces the home ranges of the giant panda and tufted deer (Fig. 3b–h). Previous studies have shown that wild giant pandas rarely use habitats with high grazing disturbances (Ran et al., 2003). Livestock incursions have reduced 34% of the area of wild giant panda habitat in the WLNR (Li et al., 2017). This has also been documented with tufted deer, which shares much of its range with the giant panda (Duan, 2014). A recent study has indicated that the home range of giant panda is larger than previously thought (Qiao et al., 2019). However, the rescue effect of metapopulations is still limited by environmental factors (such as the limiting factors of slope and bamboo density) (Armsworth, 2002). Therefore, timely intervention and management in grazing activities in WLNR is necessary for wildlife conservation.

5. Conclusion

The relationship between wildlife and their environment is always inseparable in the wild. Our results indicate that the external environment plays a crucial role in shaping the distribution of forest species. We showed that terrain is the main factor affecting the distribution of forest trees, which also determines the occurrence of wildlife, especially of arboreal animals. Interspecific interactions determine the co-occurrence of wildlife. Similarly, the distribution of territorial animals is more obviously impacted by interspecific interference.

The wildlife diversity attributes to the complex landforms and diverse vegetation. Afforestation efforts should avoid monospecific forest stands and fully consider the interaction between local forest tree composition and wildlife. Grazing activity has an integrative impact on wildlife occurrence, particularly on medium- and large-sized mammals (e.g. giant panda and tufted deer). As an umbrella for other wildlife, giant pandas are more sensitive to grazing disturbances. Therefore, conservation of giant pandas and other species in the nature reserve not only requires restoring populations and habitat protection, but also reducing grazing and changing to intensive animal husbandry. In addition, since wildlife occurrence was influenced significantly by species interactions more than by the effect of a single umbrella species (i.e. giant panda in this case), we argue that reserve design should include a consideration of a combination of multiple umbrella species rather than a single. We suggested comprising both forest plants and wildlife with higher sensitivity to environmental change and interspecific interactions. The view of umbrella combination could be a reference in planning conservation strategy.

Conflicts of interest

The authors declare no conflict of interest.

Acknowledgements

We are grateful to the staff of WNNR during the investigation.

Funding: This research was financially supported by the program "Research and demonstration of giant panda habitat restoration technology" of Major Scientific Research Achievements Project of Beijing Forestry University(2017CGP006), and "Reintroduction Technologies and Demonstration of Extremely Rare Wild Plant Populations" of National Key Research and

Development Program (2016YFC0503106) to J.Q.L. and subsidized by the Ministry of Science and Technology of Taiwan (grant number: MOST 105–2628-B-003–001-MY3 and MOST 105–2628-B-003–002-MY3) and National Taiwan Normal University (NTNU) to P.C.L.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00726>.

References

- Alexander, J.S., Zhang, C., Shi, K., Riordan, P., 2016. A granular view of a snow leopard population using camera traps in Central China. *Biol. Conserv.* 197, 27–31.
- Armstrong, P.R., 2002. Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. *Ecology* 83, 1092–1104.
- Ashton, L.A., Barlow, H.S., Nakamura, A., Kitching, R.L., Press, I.N., 2015. Diversity in tropical ecosystems: the species richness and turnover of moths in Malaysian rainforests. *Insect Conserv. Divers.* 8, 132–142.
- Carver, B.D., Kennedy, M.L., Houston, A.E., Franklin, S.B., 2011. Assessment of temporal partitioning in foraging patterns of syntopic Virginia opossums and raccoons. *J. Mammal.* 92, 134–139.
- Dinata, Y., Nugroho, A., Haidir, I.A., Linkie, M., 2008. Camera trapping rare and threatened avifauna in west-central Sumatra. *Bird. Conserv. Int.* 18, 30–37.
- Duan, L.J., 2014. Study on Activity and Habitat Use of Giant Panda and its Sympatric Species in Wanglang Nature Reserve. Beijing Forestry University, Beijing, China.
- Dubowy, P.J., 1988. Waterfowl communities and seasonal environments: temporal variability in interspecific competition. *Ecology* 69, 1439–1453.
- Gestich, C.C., Arroyo-Rodríguez, V., Ribeiro, M.C., da Cunha, R.G.T., Setz, E.Z.F., 2019. Unraveling the scales of effect of landscape structure on primate species richness and density of titi monkeys (*Callicebus nigrifrons*). *Ecol. Res.* 34, 150–159.
- Gray, T.N.E., 2018. Monitoring tropical forest ungulates using camera-trap data. *J. Zool.* 305, 173–179.
- Hu, L., 2013. Activity Rhythms of Red Deer and Roe Deer and Group Patterns of Deer Based on Camera Trapping. Beijing Forestry University, Beijing, China.
- Hull, V., Zhang, J., Zhou, S., Huang, J., Viña, A., Wei, L., Tuanmu, M.N., Li, R., Liu, D., Xu, W., 2014. Impact of livestock on giant pandas and their habitat. *J. Nat. Conserv.* 22, 256–264.
- Johnson, C.J., Boyce, M.S., Mulders, R., Gunn, A., Gau, R.J., Cluff, H.D., Case, R.L., 2004. Quantifying patch distribution at multiple spatial scales: applications to wildlife-habitat models. *Landscape Ecol.* 19, 869–882.
- Kang, D.W., Wang, X.R., Li, J.Q., 2017. Resting site use of giant pandas in Wanglang Nature Reserve. *Sci. Rep.* 7, 13809.
- Kang, D.W., Wang, X.R., Yang, H.W., Duan, L.J., Li, J.Q., 2014. Habitat use by giant panda in relation to man-made forest in Wanglang nature reserve of China. *Environ. Sci. Pollut. Res.* 21, 13440–13445.
- Kang, D.W., Zhao, L.J., Song, G.H., 2011. Competition relationship between giant panda and livestock in Wanglang national nature reserve, Sichuan. *J. Northeast For. Univ.* 39, 74–76.
- Kühl, H.S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Diegues, P., Bocksberger, G., McElreath, M.B., Agbor, A., Angedakin, S., Ayimisin, E.A., Bailey, E., Barubiyo, D., Bessone, M., Brazzola, G., Chancellor, R., Cohen, H., Coupland, C., Danquah, E., Deschner, T., Dowd, D., Dunn, A., Egbe, V.E., Eshuis, H., Goedmakers, A., Granjon, A.C., Head, J., Hedwig, D., Hermans, V., Imong, I., Jeffery, K.J., Jones, S., Junker, J., Kadam, P., Kambere, M., Kambi, M., Kienast, I., Kujirakwinja, D., Langergraber, K.E., Lapuente, J., Larson, B., Lee, K., Leinert, V., Llana, M., Maretti, G., Marrocoli, S., Martin, R., Mbi, T.J., Meier, A.C., Morgan, B., Morgan, D., Mulindahabi, F., Murai, M., Neil, E., Niyigaba, P., Ormsby, L.J., Orume, R., Pacheco, L., Piel, A., Preece, J., Regnaut, S., Rundus, A., Sanz, C., van Schijndel, J., Sommer, V., Stewart, F., Tagg, N., Vendras, E., Vergnes, V., Welsh, A., Wessling, E.G., Willie, J., Wittig, R.M., Yuh, Y.G., Yurkiw, K., Zuberbühler, K., Kalan, A.K., 2019. Human impact erodes chimpanzee behavioral diversity. *Science* 363, 1453–1455.
- Li, B.B.V., Pimm, S.L., Li, S., Zhao, L.J., Luo, C.P., 2017. Free-ranging livestock threaten the long-term survival of giant pandas. *Biol. Conserv.* 216, 18–25.
- Li, S., Wang, D.J., Bu, H.L., Liu, X.G., Jin, T., 2016. Camera-trapping survey on the mammal diversity of the laohegou nature reserve, Sichuan province. *Acta Theriol. Sin.* 36, 282–291.
- Li, S., Wang, D.J., Xiao, Z.S., Li, X.H., Wang, T.M., Feng, L.M., Wang, Y., 2014. Camera-trapping in wildlife research and conservation in China: review and outlook. *Biodivers. Sci.* 22, 685–695.
- Li, X., Nie, Y., Song, X., Zhang, R., Wang, G., 2011. Patterns of species diversity and functional diversity along the south to north-facing slope gradient in a sub-alpine meadow. *Community Ecol.* 12, 179–187.
- Marshall, J.P., Bleich, V.C.A., Nancy, G., 2008. Evidence for interspecific competition between feral ass *Equus asinus* and mountain sheep *Ovis canadensis* in a desert environment. *Wildl. Biol.* 14, 228–236.
- McKee, J.K., Sciullia, P.W., Foccea, D., Waite, T.A., 2004. Forecasting global biodiversity threats associated with human population growth. *Biol. Conserv.* 115, 161–164.
- Mitchell, M.G.E., Bennett, E.M., Gonzalez, A., 2014. Agricultural landscape structure affects arthropod diversity and arthropod-derived ecosystem services. *Agric. Ecosyst. Environ.* 192, 144–151.
- Morelli, F., Tryjanowski, P., 2015. No species is an island: testing the effects of biotic interactions on models of avian niche occupation. *Ecol. Evol.* 5, 759–768.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B.D., Kent, J., 2000. Biodiversity hotspot for conservation priorities. *Nature* 403, 853–858.
- Nakashima, Y., Fukasawa, K., Samejima, H., 2018. Estimating animal density without individual recognition using information derivable exclusively from camera traps. *J. Appl. Ecol.* 55, 735–744.
- Ohashi, H., Saito, M., Horie, R., Tsunoda, H., Noba, H., Ishii, H., Kuwabara, T., Hiroshige, Y., Koike, S., Hoshino, Y., 2014. Erratum to: differences in the activity pattern of the wild boar *Sus scrofa* related to human disturbance. *Eur. J. Wildl. Res.* 60, 567–567.
- Qiao, M., Connor, T., Shi, X., Huang, J., Huang, Y., Zhang, H., Ran, J., 2019. Population genetics reveals high connectivity of giant panda populations across human disturbance features in key nature reserve. *Ecol. Evol.* 9, 1809–1819.
- Ran, J., Liu, S., Wang, H., Sun, Z., Zeng, Z., 2003. Effect of grazing on giant pandas' habitat in yele nature reserve. *Acta Theriol. Sin.* 23, 288–294.
- Rich, L.N., Miller, D.A.W., Robinson, H.S., McNutt, J.W., Kelly, M.J., 2017. Carnivore distributions in Botswana are shaped by resource availability and intraguild species. *J. Zool.* 303, 90–98.
- Rogers, P.M., Myers, K., 1980. Animal distributions, landscape classification and wildlife management, coto donana, Spain. *J. Appl. Ecol.* 17, 545–565.
- Rong, Z.L., Liu, X.M., Zhao, C.Y., He, L.W., Liu, J.J., Gao, Y.F., Zang, F., Xu, H.J., Guo, Z.X., Mao, Y.H., 2019. Evaluating giant panda as a surrogate species for conservation co-occurring species in the Baishuijiang National Nature Reserve. *Environ. Sci. Pollut. Res.* 26, 8939–8948.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Sellan, G., Thompson, J., Majalap, N., Brearley, F.Q., 2019. Soil characteristics influence species composition and forest structure differentially among tree size classes in a bornean heath forest. *Plant Soil* 1–13.
- Sharpe, P.J., Baldwin, A.H., 2013. Wetland plant species richness across estuarine gradients: the role of environmental factors and the mid-domain effect. *Aquat. Bot.* 107, 23–32.
- Stewart, F.E.C., Fisher, J.T., Burton, A.C., Volpe, J.P., 2018. Species occurrence data reflect the magnitude of animal movements better than the proximity of animal space use. *Ecosphere* 9, e02112.

- Tang, X.P., 2005. Analysis of the current situation of China's nature reserve network and a draft plan for its optimization. *Biodivers. Sci.* 13, 81–88.
- Tian, C., Li, J., Yang, X., Yu, L., Yuan, D., Li, Y., 2018. Preliminary surveys of wild animals using infrared camera in Wanglang national nature reserve, Sichuan province. *Biodivers. Sci.* 26, 620–626.
- Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., Packer, C., 2017. Future threats to biodiversity and pathways to their prevention. *Nature* 546, 73–81.
- Tobler, Mathias, W., POWELL, George, V.N., 2013. Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. *Biol. Conserv.* 159, 109–118.
- Wang, M.J., Li, J.Q., 2008. Research on habitat restoration of giant panda after a grave disturbance of earthquake in Wanglang nature reserve, Sichuan province. *Acta Ecol. Sin.* 28, 5848–5855.
- Wangdi, T., Tobgay, S., Dorjee, K., Dorji, K., Wangyel, S., 2018. The distribution, status and conservation of the himalayan musk deer *moschus chrysogaster* in Sakteng wildlife sanctuary. *Glob. Ecol. Conserv.* 17, e00466.
- Weyde, L.K.V.D., Mbisana, C., Klein, R., 2018. Multi-species occupancy modelling of a carnivore guild in wildlife management areas in the Kalahari. *Biol. Conserv.* 220, 21–28.
- Yuh, Y.G., Dongmo, Z.N., N'Goran, P.K., Ekodeck, H., Mengamenya, A., Kuehl, H., Sop, T., Tracz, W., Agunbiade, M., Elvis, T., 2019. Effects of land cover change on great apes distribution at the lobeke national park and its surrounding forest management units, South-East Cameroon. A 13-year time series analysis. *Sci. Rep.* 9, 1445.
- Zang, Z., Shen, G., Ren, G., Wang, C., Feng, C., Xu, W., Xie, Z., Chen, Q., Yang, X., Li, J., 2017. Thermal habitat of giant panda has shrunk by climate warming over the past half century. *Biol. Conserv.* 211, 125–133.
- Zhao, Q., Yang, J., Yang, X.Z., Tian, L.H., He, X.J., 2007. A survey of disturbance of giant panda habitat in TaiBaishan nature reserve. *For. Invest. Des.* 04, 63–66.
- Zhao, Z.J., 2013. The Responses of *Abies Faxoniana* and *Picea Purpurea* to Climate Factors in Subalpine of Western Sichuan Province, China. Beijing Forestry University, Beijing, China.