




CONTRIBUTED PAPER

Complex effects of habitat amount and fragmentation on functional connectivity and inbreeding in a giant panda population

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Article impact statement: Habitat amount and fragmentation have nonlinear effects on gene flow and inbreeding and are best managed at intermediate levels for pandas.

Abstract

The relationships between habitat amount and fragmentation level and functional connectivity and inbreeding remain unclear. Thus, we used genetic algorithms to optimize the transformation of habitat area and fragmentation variables into resistance surfaces to predict genetic structure and examined habitat area and fragmentation effects on inbreeding through a moving window and spatial autoregressive modeling approach. We applied these approaches to a wild giant panda population. The amount of habitat and its level of fragmentation had nonlinear effects on functional connectivity (gene flow) and inbreeding. Functional connectivity was highest when approximately 80% of the surrounding landscape was habitat. Although the relationship between habitat amount and inbreeding was also nonlinear, inbreeding increased as habitat increased until about 20% of the local landscape contained habitat, after which inbreeding decreased as habitat increased. Because habitat fragmentation also had nonlinear relationships with functional connectivity and inbreeding, we suggest these important responses cannot be effectively managed by minimizing or maximizing habitat or fragmentation. Our work offers insights for prioritization of protected areas.

KEYWORDS

conservation biology, conservation genetics, gene flow, genetic diversity, giant panda, habitat fragmentation, inbreeding, landscape ecology, landscape genetics

Efectos Complejos de la Cantidad de Hábitat y la Fragmentación sobre la Conectividad Funcional y la Endogamia en una Población de Panda Gigante

Resumen: Las relaciones entre la cantidad de hábitat y el nivel de fragmentación con la conectividad funcional y la endogamia no son muy claras. Por lo tanto, utilizamos algoritmos genéticos para optimizar la transformación de la superficie de hábitat y variables de fragmentación en superficies de resistencia para predecir la estructura genética y examinamos los efectos de la superficie de hábitat y la fragmentación sobre la endogamia por medio de un método de ventana móvil y de modelado espacial autorregresivo. Aplicamos estos métodos a una población de panda gigante. La cantidad de hábitat y su nivel de fragmentación tuvo efectos no lineales sobre la conectividad funcional (flujo génico) y la endogamia. La conectividad funcional fue más alta cuando aproximadamente 80 por ciento del paisaje circundante era hábitat. Aunque la relación entre la cantidad de hábitat y la endogamia tampoco fue lineal, la endogamia incrementó hasta que casi 20% del paisaje local contenía hábitat, después de lo cual la endogamia decreció a medida que incrementó el hábitat. Debido a que la fragmentación de hábitat tampoco tuvo relaciones lineales con la diversidad funcional y la endogamia, sugerimos que estas respuestas importantes no pueden ser manejadas eficientemente minimizando o maximizando el hábitat o la fragmentación. Nuestro trabajo aporta conocimientos para la priorización de áreas protegidas.

PALABRAS CLAVE:

Biología de la conservación, diversidad genética, endogamia, flujo génico, fragmentación de hábitat, genética de la conservación, genética del paisaje, panda gigante

标题: 生境面积及破碎化对大熊猫种群功能连通性和近亲繁殖的复杂影响**摘要:**

野生动物的生境面积和破碎化程度与其种群功能连通性和近亲繁殖之间的关系尚不清楚。因此,我们以野生大熊猫种群为研究对象,利用遗传算法将生境面积和破碎化程度优化为阻力面来预测其种群遗传结构,并基于移动窗口和空间自回归模型来分析生境面积和破碎化对其种群近亲繁殖的影响。结果显示:生境面积及其破碎化程度对其种群功能连通性(基因流动)和近亲繁殖具有非线性影响。当景观面积的80%为适宜生境时,其种群功能连通性最高。虽然生境面积与近亲繁殖之间的关系也是非线性的,但是当生境面积达到局域景观大约20%时,近亲繁殖随生境面积的增加而增加,然后近亲繁殖水平会随着生境面积的增加而逐渐降低。同时,由于生境破碎化与功能连通性和近亲繁殖也具有非线性关系,我们认为不能简单地通过使生境面积最大化或生境破碎最小化来实现对野生大熊猫种群功能连通性和近亲繁殖的有效管理。这项研究也为保护区的优先建立和管理提供科学参考。

关键词:

生境破碎化, 基因流动, 保护遗传学, 保护生物学, 大熊猫, 景观遗传学, 景观生态学, 遗传多样性, 近亲繁殖

INTRODUCTION

It is generally recognized that habitat amount should be maximized in conservation endeavors (Franklin et al. 2000; Villard & Metzger 2014; Fahrig 2017). However, the relative importance of habitat fragmentation has been the subject of hot debate (e.g., Fahrig 2017; Fletcher et al. 2018; Fahrig et al. 2019). In a review of 118 studies, Fahrig (2017) found that most ecological effects of habitat fragmentation were not significant and most that were significant were positive. Other studies show that habitat fragmentation has clear negative effects on several ecological responses and ecosystem functions (Haddad et al. 2015; Fletcher et al. 2018).

Habitat loss and fragmentation affect the successful dispersal and reproduction of individuals across landscapes (i.e., functional connectivity or gene flow). Functional connectivity between populations maintains levels of genetic diversity necessary to adapt to changing environmental conditions (Frankham 1995; Eizaguirre & Baltazar-Soares 2014; Bay et al. 2017). Maintenance of functional connectivity among discrete habitat patches across the landscape also allows recolonization following extirpations (Hanski 1998; Hanski & Gaggiotti 2004). Thus, it is vital for the preservation of genetic and species diversity, key conservation goals that have been emphasized in the post-2020 Global Biodiversity Framework (Smart & Peña Moreno 2019; CBD 2020).

Keyghobadi (2007) conducted a review of 32 empirical studies that compared the genetic structure of populations in more and less fragmented landscapes and found that 69% showed increased genetic differentiation (reduced functional connectivity) in fragmented landscapes and 31% showed either no effect or greater differentiation in control landscapes. Most of the

reviewed studies conflated habitat loss and fragmentation and did not disentangle their effects, which is a frequent problem in habitat fragmentation ecological research (Keyghobadi 2007; Smith et al. 2009). Although the directional effects of habitat amount on functional connectivity have been less explicitly researched, and are often conflated with fragmentation, it is generally assumed that habitat loss reduces connectivity (Soons et al. 2005; Dytham & Travis 2012). Regarding the relative importance of habitat loss versus its fragmentation on functional connectivity, opposing conclusions have even been reported in simulation studies (Cushman et al. 2012; Jackson & Fahrig 2016).

Landscape genetics methods, which combine techniques from landscape ecology and population genetics (Manel et al. 2003), are ideal for studying the effects of habitat amount and fragmentation on functional connectivity. Typically, environmental variables are transformed into new surfaces based on hypothesized resistances to animal movements that result in an isolation by resistance (IBR) pattern (Manel & Holderegger 2013). We developed a method that combines species distribution modeling (SDM) and landscape genetics to estimate habitat amount and a suite of habitat fragmentation variables as continuous resistance layers across the landscape and investigated their effects on functional connectivity in a wildlife population. We used genetic algorithms to optimize the transformation of these continuous variables into resistance surfaces that predict observed genetic structure, implemented through the ResistanceGA R package (Peterman 2018). We also examined habitat amount and fragmentation effects on inbreeding through a moving window and spatial autoregressive modeling approach. We tested our methods on a wild population of giant pandas (*Ailuropoda melanoleuca*). Giant pandas are habitat

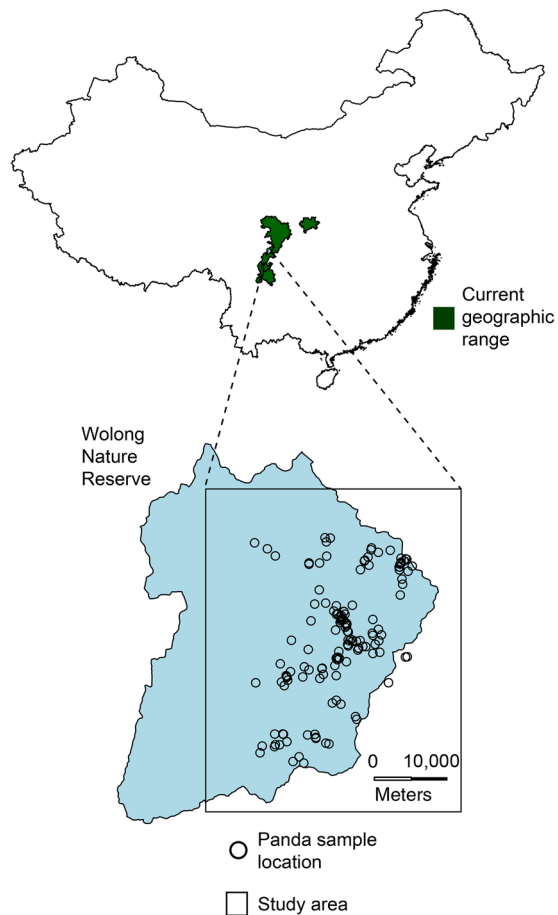


FIGURE 1 Study area and sample locations inset on a map of continental China and the current giant panda geographic range

specialists and are sensitive to anthropogenic disturbance (Schaller 1985). Giant pandas exist in small remnant populations that face anthropogenic habitat degradation and intensive conservation effort (Xu et al. 2017). Our results are directly applicable to the conservation planning of protected areas to maximize functional connectivity and minimize inbreeding in panda populations across the landscape, and our methods are applicable to many other wildlife species.

METHODS

Study area

Wolong Nature Reserve is an approximately 2000-km² national protected area centrally situated in the panda's extant range (Figure 1). There are approximately 150 giant pandas in the reserve (Qiao et al. 2019). Panda habitat in the reserve consists of understory bamboo forests below 4000 m elevation (Linderman et al. 2005). Besides forest and elevation requirements, other important habitat variables include terrain ruggedness and anthropogenic disturbance levels (Hull et al. 2014). Rugged terrain induces additional energy expenditure that pandas preferentially avoid (Nie et al. 2015), and human activity

negatively affects panda occurrence (Zeng et al. 2019). These variables influence the amount of habitat and levels of habitat fragmentation in the landscape surrounding panda occurrence locations (Liu et al. 2016).

Noninvasive fecal sampling

Fecal samples were collected throughout 2015 and 2016 with a systematic sampling design. We subdivided known and potential habitat areas throughout the reserve, based on suitable elevation ranges (1100–4000 m), into 2-km² survey cells that were searched in a zigzag manner by experienced field workers and local guides. Fresh panda feces, judged by the status of the outer mucosal membrane, were collected, stored in sterile plastic bags, and frozen within 8 h of collection.

Genetic analyses

Seven microsatellite loci were selected for analysis based on levels of polymorphism, lack of genotyping error, and high amplification success rate even when feces were exposed to natural weather conditions for extended periods (Huang et al. 2015). We genotyped 142 unique pandas across the reserve. Details of laboratory methods and quality control are in Appendix S1.

To calculate genetic distance between individuals, we used codominant genotypic distance implemented through GenAlEx, which effectively measures genetic structure when the number of loci available is small (Peakall & Smouse 2006, 2012; Draheim et al. 2015). We allowed missing information at one locus to maximize sample size. If an individual was captured multiple times across the study area, its location for the landscape genetic analyses was defined as the median x and y coordinates from its capture locations. We used the median to avoid excessive placement of individuals in unrealistic habitat locations on the landscape.

To calculate inbreeding, we calculated Wright's inbreeding coefficient (F_{IS}) corrected for small sample size with the *gstudio* R package (Wright 1965; Dyer 2012; R Core Development Team 2019). This metric corresponds to the level of observed heterozygosity relative to expected heterozygosity in the population; positive values indicate increased inbreeding and negative values indicate decreased inbreeding. To define the local populations within which to calculate F_{IS} , we used a moving-window approach across the landscape with the same optimized spatial scale (window size) used in our functional-connectivity modeling to maintain consistency (details in Appendix S5 and Peterman [2018]).

Giant panda presence data

In training our habitat models, we used georeferenced giant panda sign (scat, hair) locations gathered from the fourth national giant panda survey, a consistent range-wide sampling effort (China). We selected only presence locations within our

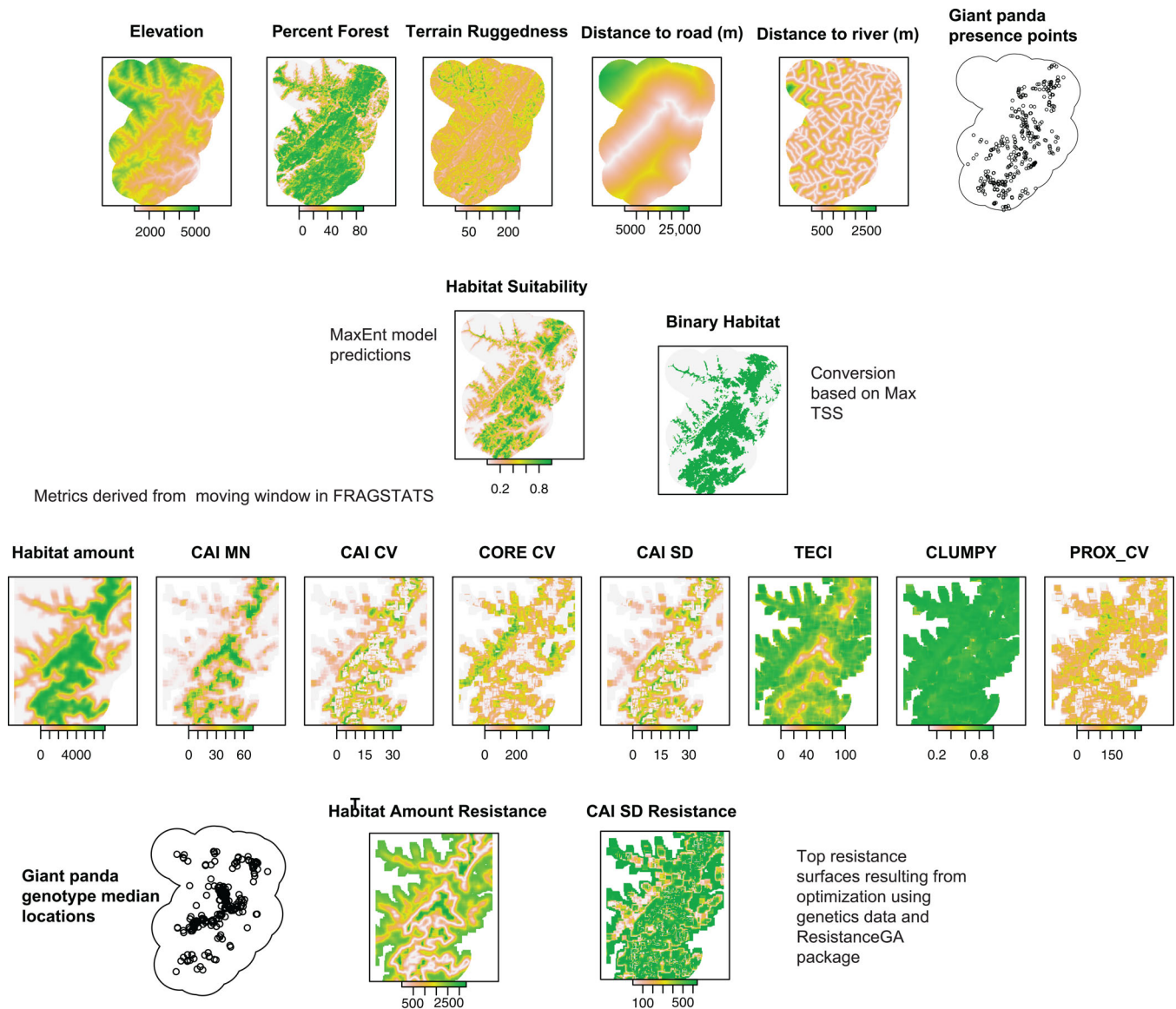


FIGURE 2 Flowchart of the process and intermediary outputs in the development of a map of landscape resistance to panda gene flow across the study area in China, starting with raw environmental variables and giant panda presence data set. For more details on each step and definitions of abbreviations, see METHODS

noninvasive genetics survey extent ($n = 360$) (Figure 2). This subset of the survey presence data was collected throughout Wolong in 2012. We tested the ability of the models to predict giant panda habitat across our study area based on the locations of fecal samples collected for our genetic analyses from 2015 to 2016. We thus trained models with an independently collected data set and evaluated them based on our genetic sample locations—the most relevant locations for our later landscape genetics analyses.

MaxEnt modeling

We used elevation, aspect, terrain ruggedness, percent tree cover, distance to a main road, and distance to a stream or

river as predictors of giant panda habitat (variable sources in Appendix S3). We used the MaxEnt modeling algorithm implemented through dismo R package to relate giant panda presence locations to environmental predictors (Hijmans et al. 2017). This species distribution model has good predictive accuracy (Elith & Graham 2009). Another advantage of MaxEnt is that its formulation as a presence-only algorithm does not require known absence locations, but instead compares presence locations with background environmental conditions described by random points across the study area (Phillips et al. 2006). The algorithm makes use of machine-learning techniques to minimize the relative entropy in the predicted suitability between the presence and background locations (Elith et al. 2011).

We randomly selected 100,000 points across our study area as background locations. This sample was 10 times the default

number generated by MaxEnt. Our study area had a large number of raster cells (>10 million), so we chose this number of points to improve estimates of background conditions (Renner & Warton 2013). We trained the MaxEnt model with these background locations, the presence locations from the fourth national survey, and the environmental variables. We then used the model and environmental variables to predict presence (1) and absence (0) of habitat across the study area and tested model accuracy using the presence locations from our fecal genetics survey and 68,270 random points that served as background locations. We chose this number of background locations so the ratio of our model-training background locations versus model-testing background locations matched the ratio of model-training presence locations versus model-testing presence locations used in our modeling procedure. The total model-training and model-testing extents remained the same—only the number of presence and background points differed. Several accuracy statistics, including area under the receiver operator curve (AUC), true skill statistic (TSS), and correlation between predicted suitability values between test presences and test background locations (Cor), were used to evaluate model performance in predicting habitat. In using these statistics, we assumed the majority of our pseudoabsence locations could be interpreted as true absences. Finally, we converted the continuous habitat surface into a binary habitat or not habitat map around the suitability threshold that maximized the value of the TSS (Figure 2). This threshold reflects the point at which omission and commission errors in predicting the relative density of panda locations were minimized to create the most accurate depiction of habitat across the landscape (Allouche et al. 2006).

Habitat amount and fragmentation

To create variables measuring habitat amount and fragmentation that could be used to predict gene flow, we needed spatially explicit estimates that would capture these values in the relevant surrounding landscape for each cell in our study area. To achieve this, we used a moving-window approach on the binary habitat–not habitat map in which we calculated the amount of habitat and its level of fragmentation (see below) in the area within a certain distance threshold surrounding the focal cell, which then took those values. We optimized this threshold at 42 cells (1149 m) away from the focal cell, resulting in an 85- × 85-cell (2325 × 2325 m) matrix for the calculation of habitat amount and fragmentation. This threshold was optimized using the `SS_optim.scale` function in the `ResistanceGA` package in R (details in Appendix S5 and Peterman [2018]). The resulting local landscape window of 5.40 km² fell within the typical home range size of pandas in this region (Connor et al. 2016).

We evaluated seven habitat fragmentation variables: total edge contrast index (TECI), clumpiness index (CLUMPY), proximity index coefficient of variation (PROX_CV), mean core area index (CAI_MN), core area index coefficient of variation (CAI_CV), core area index SD (CAI_SD), and core area coefficient of variation (CORE_CV) (McGarigal et al. 2012). We chose these metrics because they have low correlation with the

amount of habitat in a given landscape and the capacity to differentiate between landscapes featuring a wide range of habitat fragmentation levels (Wang et al. 2014). We tested the performance of two definitions of edge depth in calculating the core area metrics—one cell (27.35 m) and seven cells (191.45 m)—based on the assumption that core habitat starts at 27.35 m from an edge or 191.45 m from an edge, respectively. We have observed panda scat <50 m from the edge of habitat patches (e.g., <50 m from a grassland, which is not habitat), which supports the former edge-depth definition, whereas the latter definition incorporates the majority of step lengths derived from GPS-telemetry location fixes at 3-h intervals in five pandas (Hull et al. 2015). The CAI metrics measure the percent habitat that is core habitat across habitat patches. The CORE_CV metric is the coefficient of variation of the amount of core area in each patch. For the edge contrast metric (TECI), we defined the contrast between habitat and not habitat as the maximum possible (contrast = 1). Because we had only two classes in our landscape, TECI was a measure of the number of edges in each local window. The CLUMPY metric measures the number of like adjacencies observed between habitat cells in the landscape compared with the number that would be expected given a random distribution of the habitat cells. We used the moving-window functionality in FRAGSTATS to calculate all metrics with the 85- × 85-cell window with an eight-cell neighborhood (McGarigal et al. 2012). The amount of habitat in the window was calculated by summing the number of habitat cells in the same 85- × 85-cell window with the focal function in the raster R package (Hijmans 2020).

Landscape genetic analyses

To relate landscape variables to the observed pattern of genetic distances between individuals, variables must be transformed into a resistance surface (Spear et al. 2010). This surface represents the hypothesized effect of the landscape variable on gene flow. The relative support of a given variable and its transformation to a resistance surface must be evaluated relative to other hypothesized variables or transformations, with the observed genetic distances as the response variable to resistance distances between the genetic sample locations. We used the `ResistanceGA` package to streamline this process and evaluate the effects of habitat amount and fragmentation on genetic distance (Peterman 2018). This package uses genetic algorithms and maximum likelihood population mixed effects (MLPE) models to test multiple transformations of input variables into resistance surfaces and evolve to better solutions based on how well the proposed resistance surface predicts genetic distance (McRae 2006; Peterman et al. 2014). We modeled movement with `Circuitscape`, which evaluates probabilities of movement at each cell between sample locations based on the resistance values of the surrounding cells (McRae 2006).

By employing MLPE models, the effects of environmental resistance surfaces on movement can be separated from the random effects specified as the pairwise dependence of observations. Likely due to this flexibility, MLPE models have

tested as the best method of model selection among those commonly used in landscape genetics research (Peterman et al. 2019). ResistanceGA also performs well in recovering the correct resistance surface relative to other landscape genetics methods in simulated environments (Peterman et al. 2019). We considered all eight possible resistance transformation equations in the package, which each takes a maximum and shape parameter to define the transformation and can be varied to explore a variety of transformation curves (Peterman 2018). The genetic algorithm randomly generates new transformations through the mutation and recombination of the maximum and shape parameters in every generation. We used the loglikelihood of the resulting MLPE model as the fitness function to optimize. In evaluating models, we defined the number of parameters (k) as 3: the surface itself, maximum value of the transformation, and shape of the transformation.

We evaluated the habitat amount, our continuous habitat suitability index, and eight habitat fragmentation metric surfaces individually with the SS_optim function. We also evaluated a model including only Euclidean distance between sample locations (isolation-by-distance model) and a completely null model based on the assumption of panmixia. Before optimization, we aggregated the cell size of these surfaces by a factor of 8 to a size of 218.8 m based on the mean value of the small cells due to the computational demand of these cells (27.35 m cell size). This is unlikely to affect results (McRae 2006; Cushman & Landguth 2010). We ranked the performance of these single variable surface models according to their AIC corrected for the number of sample individuals and parameters (AICc) in each MLPE (Akaike 1974). We considered any surface that had an AICc with a difference of <4 from the top surface as competitive (Burnham & Anderson 2004; Beninde et al. 2016). We then built multivariable resistance surfaces by transforming and adding together every possible combination of these competitive variable surfaces with the MS_optim function in ResistanceGA. In this function, the relative weights of each surface's contribution to the final resistance surface are also optimized. If any pair of the competitive single variable surfaces had a Pearson's correlation value >0.5 , we considered only the higher ranked surface of the pair in the multi-surface model due to collinearity and the need to disentangle habitat amount from fragmentation effects (Dormann et al. 2013; Wang et al. 2014). We ranked all final single-surface and multi-surface variable combinations and transformations according to AICc. To facilitate ease of interpretation of the final transformations of the habitat amount and fragmentation surfaces, we inversed the resistance transformation plots to depict functional connectivity instead.

To examine the effects of habitat amount and fragmentation on inbreeding (F_{IS}), we fitted spatial autoregressive (SAR) models to the F_{IS} values for each local population and habitat amount or fragmentation layer with the spatialreg R package (Bivand et al. 2008). Each local population was defined as those individuals in the local landscape window (5.4 km²) surrounding a cell. This was kept consistent with the optimized window described above in the landscape genetics analyses to facilitate comparisons. We defined the distance at which spatial autocorrelation was estimated and accounted for (Bivand et al.

TABLE 1 Most supported (change in Akaike's information criterion corrected for small sample size [AICc] <4) maximum-likelihood population mixed-effects model (MLPE) results from ResistanceGA outputs relating habitat amount and fragmentation effects on giant panda gene flow, ranked by increasing AICc, and most supported spatial autoregressive model (SAR) results relating habitat fragmentation to Wright's inbreeding (F_{IS}), ranked by increasing AICc and habitat amount model

Transformed surfaces in MLPE model	Parameters	AICc	Change in AICc	Conditional R ²
CAI_SD ^a	4	44,206.18	0.00	0.348793
Habitat Amount	4	44,208.91	2.74	0.367357
Surfaces in SAR model				
CAI_MN ^{b,c} x TECI ^c	8	-14,616.37	0.00	
Habitat Amount ^c	6	-14,580.37	36	

Abbreviations: CAI, core area index; MN, mean; SD, standard deviation; TECI, total edge contrast index.

^aMetric calculated with edge depth of 191.45 m.

^bMetric calculated with edge depth of 27.35 m.

^cModels included quadratic terms.

2008) by plotting a variogram fitted to the spatial F_{IS} data and by visually determining this distance threshold at approximately 2000 m (Appendix S7) (Bivand et al. 2008). Because we used spatial regression for this response, we directly evaluated the support for including linear versus nonlinear terms in the models incorporating each habitat and fragmentation layer by creating two separate models per surface. We ranked models according to AICc and created multivariate models if models based on separate single surfaces were within four AICc of each other.

RESULTS

Functional connectivity and inbreeding responded nonlinearly to amount of habitat (Figure 3). There was support for three models incorporating the optimized transformations of two different variables into resistance surfaces that explained genetic connectivity, of which habitat amount ranked second based on AICc (Table 1). For habitat amount, an inverse–reverse Ricker transformation was most associated with functional connectivity across the landscape (Figure 3). Functional connectivity increased as the number of habitat cells increased until about 80% (or 4.34 km²) of the surrounding landscape (5.40 km²) was habitat, but it rapidly decreased further increases in habitat (Figure 3). Inbreeding increased slightly as habitat increased until about 25% (1.35 km²) of the surrounding landscape was habitat, and it decreased as habitat further increased.

Among the top models of functional connectivity was the standard deviation of the core area index between habitat patches (CAI_SD) in the surrounding landscape (Table 1 & Appendix S6). The optimized transformation of CAI_SD was nonlinear and resulted from inverse Ricker equations (Figure 3a). Specifically, local landscape windows with no

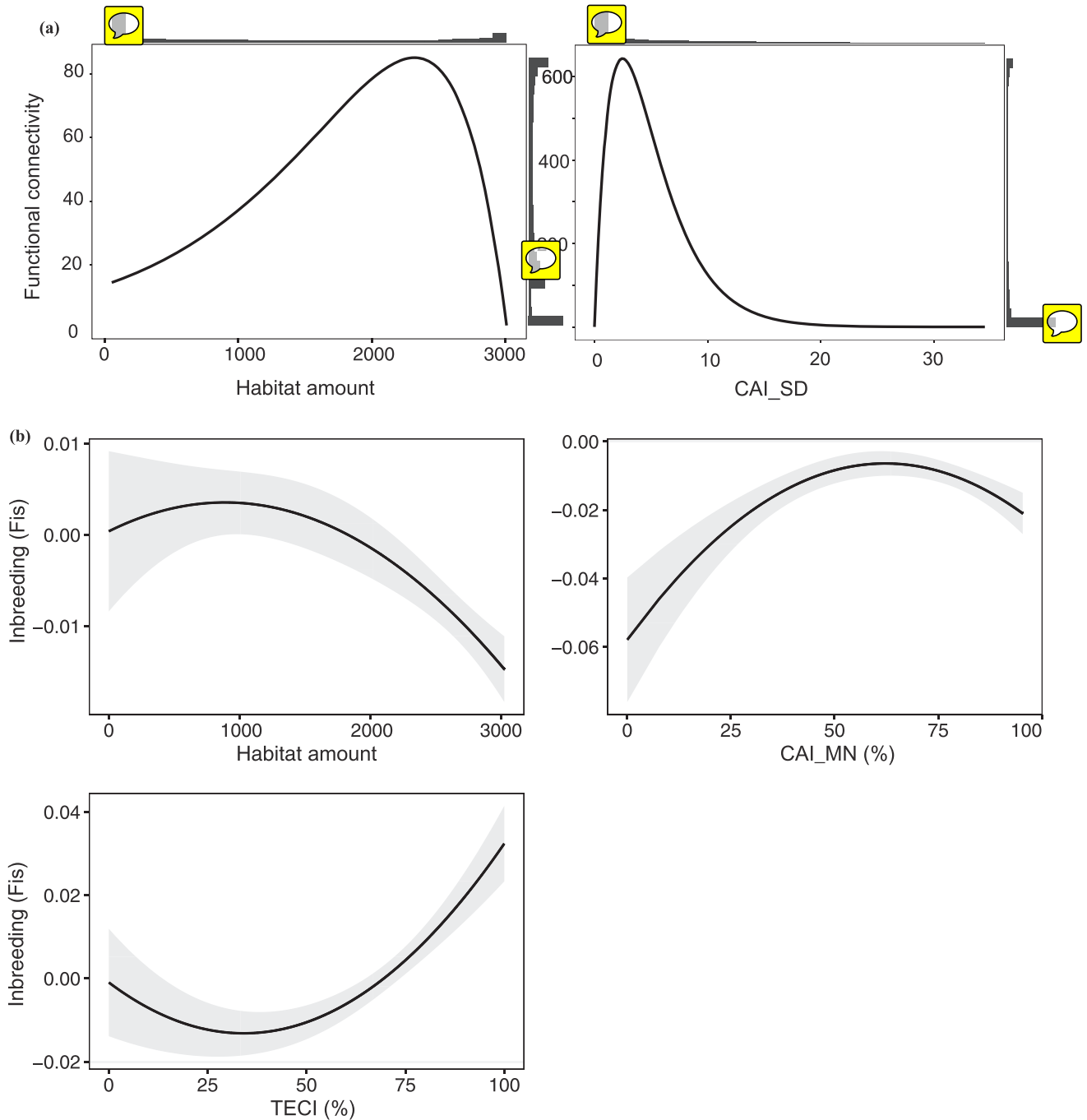


FIGURE 3 (a) Functional connectivity (inverse of resistance) response curves to habitat amount and fragmentation metrics in the most supported maximum-likelihood population effects models (histograms, distribution of raw data values for each axis; CAI SD, standard deviation of the core area index) and (b) inbreeding (measured as Wright’s inbreeding coefficient) response curves to fragmentation metrics in the most supported spatial autoregressive models (shading, 95% CIs; CAI MIN, minimum of the core area index; TECI, total edge contrast index) of a population of pandas. In panel (b), habitat amount was not among the top models but is presented for comparison

variation in the relative amount of core area between patches resulted in low connectivity, but this connectivity rapidly increased until it was maximized at an SD in the core area index of about 2.5. For example, when a local landscape contained two habitat patches with 60% and 56.46% core area, this local landscape would have an SD of 2.5 and the highest possible functional connectivity predicted. Further increases in heterogeneity

rapidly decreased functional connectivity until about CAI_SD = 15, which represented relatively large variation in the proportion of core area between habitat patches (e.g., two patches containing 20% and 50% core area). In other words, local landscapes entirely composed of a single patch of habitat (no variation in CAI), composed of multiple patches with matching or extremely similar CAI values, or composed of multiple

TABLE 2 Parameter coefficients from the top maximum-likelihood population mixed-effects model (MLPE) of habitat amount or fragmentation effects on functional connectivity and the top spatial autoregressive model (SAR) of habitat amount or fragmentation on inbreeding (measured as Wright's inbreeding coefficient) in a giant panda population

Model	Estimate	SE	<i>p</i>
MLPE ^a			
Intercept	9.29	0.26	<0.001
CAI_SD	0.27	0.03	0.004
SAR			
Intercept	-0.052	0.018	0.004
TECI_1	-7.2×10^{-4}	2.5×10^{-4}	0.004
TECI_1 ²	1.1×10^{-5}	2.5×10^{-6}	<0.001
CAI_MN	0.002	3.5×10^{-4}	<0.001
CAI_MN ²	-1.3×10^{-5}	2.7×10^{-6}	<0.001
Lambda ^b	0.93	0.01	<0.001

^aParameter abbreviations are defined in METHODS and Table 1.

^bSpatial autocorrelation parameter.

patches of drastically different CAI values resulted in low gene flow.

The top model fit to F_{IS} included two fragmentation metrics: the mean CAI value metric with the 27.35-m edge definition and TECI. Both these metrics had nonlinear effects on inbreeding (Figure 3b). The mean CAI metric had a nonlinear, initially positive effect on inbreeding until about 65%, after which further inbreeding decreased as CAI increased. The TECI metric indicated minimum inbreeding at around 30%, an intermediate amount of habitat edges on the landscape (Figure 3b). Although the habitat amount surface was not ranked in the top models, we also plotted the marginal effects of habitat amount on F_{IS} , which indicated some nonlinearity but minimized F_{IS} at 100% habitat in the local landscape. For the top models relating habitat amount or fragmentation to functional connectivity and inbreeding, all parameter coefficients were statistically significant (Table 2).

DISCUSSION

We, to the best of our knowledge, are the first to demonstrate a hump-shaped nonlinear effect of habitat amount and fragmentation on functional connectivity in an empirical system, although similar patterns for habitat amount were found in a simulation (Jackson & Fahrig 2016). We posit that large amounts of habitat in a local area result in more resource availability and in turn lower dispersal rates and smaller dispersal distances, which drive the negative relationship between habitat amount and functional connectivity we observed at habitat amounts of 80% or more. In theory, at high population densities and growth rates, areas with more habitat may serve as source populations from which individuals disperse across the landscape (Clobert et al. 2009; Draheim et al. 2016). Either giant panda densities in our landscape were not high enough to promote this behavior

or the number of nondispersing individuals was high enough to mask the genetic signal of individuals dispersing from the high-resource source areas. In either case, it may make sense to think of local landscapes containing more than 80% habitat as being attractive to individuals rather than as impediments to their movement (Clobert et al. 2012). Regardless of the theoretical framing of the process, our findings show that high levels of habitat indicative of high structural connectivity may result in an observable pattern of reduced functional connectivity in panda populations within the relatively short time frame of our study. Although inbreeding in local panda populations was also affected nonlinearly by habitat amount, our results indicated that the lowest inbreeding occurred at the maximum amount of habitat.

An increase in functional connectivity as fragmentation increases has been observed in empirical and theoretical studies before, likely because the probability of encountering and successfully colonizing a new habitat patch increases as fragmentation increases (Holzschuh et al. 2010; Saura et al. 2014). We found a threshold at which this trend may be reversed, however, and that higher levels of fragmentation may limit successful dispersal. In our case, this threshold occurred when patches were slightly varied in their amount of core habitat area—deviations from this optimal variance resulted in rapid decreases in functional connectivity.

Genetic diversity commonly increases as fragmentation decreases (Keyghobadi 2007; Gonzalez et al. 2020), in part because of the infusion of nonresident alleles, but nonlinear effects have rarely been identified. In our study system, we found nonlinear relationships with inbreeding in the CAI_MN and TECI metrics across that landscape. For the CAI_MN, inbreeding was minimized when all patches had zero core area on the local landscape, whereas the TECI variable coefficients suggested that inbreeding was minimized when there was a low but nonzero presence of edges on the landscape. These findings suggest there is an optimum balance between maintaining adequate habitat and allowing landscape structure with multiple smaller habitat patches and the presence of edges to minimize inbreeding. This tracks with other studies of panda ecology that show pandas may preferentially select the edges of bamboo patches for feeding (Yu et al. 2003).

Although a large-scale sampling effort was undertaken, our study system encompassed a proportionally small area of the giant panda range and only a single (2-year) sampling period. For larger scale landscape effects on genetic connectivity, sampling across distinct populations (i.e., separate mountain ranges [Zhao et al. 2013]) would be needed, but our analysis of interindividual genetic distance is a powerful tool to examine gene flow in a continuously distributed population and more valid than attempting to differentiate subpopulations within our study area (Shirk et al. 2018; Qiao et al. 2019). To examine ongoing effects of habitat structure, it will be important to sample genetics over time and conduct stratified analyses (Draheim et al. 2018). Spatial scale is also an important consideration in any ecological analysis, and its misspecification can lead to erroneous inference (Wiens 1989; Connor et al. 2019). We optimized the window size of our landscape genetics analysis with a

data-driven approach through ResistanceGA and used the same window size for the inbreeding analysis to facilitate comparison. Although an optimized window for genetic connectivity likely reflects a good scale of effect for analyzing inbreeding, there may be other important spatial scales at play. Intermediate steps in our analysis may have introduced bias. For example, the median location for individuals captured more than once could introduce bias if that location falls in an unrealistic area (which we attempted to minimize by taking the median as opposed to the mean). Also, converting continuous predictions of habitat suitability to a binary measure of habitat and not habitat was necessary to derive fragmentation metrics, but it reduced information in the habitat estimate (Guillera-Aroita et al. 2015). However, the continuous habitat suitability layer was not ranked among the top models explaining functional connectivity or inbreeding (Appendix S6).

Because most conservation projects have limited funding, our findings have significant implications for the spatial planning of habitat protection and restoration efforts. This is especially the case for threatened species facing subpopulation fragmentation like the giant panda (Xu et al. 2017). The varied thresholds we found for habitat amount and fragmentation effects on functional connectivity and inbreeding are important to consider in conservation because these thresholds suggest different optimums in the different response variables. Generally, however, having relatively high amounts of habitat to support pandas was important, which is consistent with conservation measures such as protected areas and timber harvesting bans. Large habitat areas may be especially important for pandas due to their relatively low fecundity rates, meaning that migration may play an important role in demographic and genetic connectivity and genetic diversity (Lowe & Allendorf 2010). The finding that the optimum habitat amount for functional connectivity was below 100% provides hope for the already disturbed areas of panda habitat and suggests that such areas might still be considered suitable. Thus, plans to connect isolated panda subpopulations may be more realistic and feasible than previously thought.

The protection of habitat patches versus protection of large, uninterrupted tracts of habitat has been debated for decades (Tjorve 2010). Our findings indicate that the protection of several tracts, as opposed to a single large area, of habitat may enhance functional connectivity in an obligate habitat specialist species. This may be even more effective for generalist species, which would likely be able to use unprotected areas more efficiently (Bartonova et al. 2016; Ducatez et al. 2018). Large, contiguous protected areas come with additional challenges. They are often located in areas of low conservation value (Fuller et al. 2010; Klein et al. 2015). In more productive regions, humans often concentrate at the edges of protected areas (Wittemyer et al. 2008), which may reduce functional connectivity of wildlife population in- and outside those areas. We suggest that landscapes of patchier habitat should be prioritized for conservation and restoration in a scientifically informed manner (aiming for 80% habitat that maintains adequate edges) in order to maximize giant panda population health. Applying our framework to

more species would synchronize well with the post-2020 global biodiversity framework to protect genetic, species, and ecosystem diversity (e.g., Mace et al. 2018; Smart & Peña Moreno 2019; Díaz et al. 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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