Landscape-scale giant panda conservation based on metapopulations within China’s national park system

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Historically, giant panda conservation in China has been compromised by disparate management of protected areas. It is thus crucial to address how giant panda populations can be managed cohesively on a landscape scale, an opportunity offered by China’s newly established Giant Panda National Park. Here, we evaluated giant panda populations in a metapopulation context, based on range-wide data from the Fourth National Giant Panda Survey. We delineated metapopulations by geographic range, relative abundance, and relative density and assessed the extent of human disturbance each metapopulation faced. We found density-dependent and disturbance-influenced effects on habitat selection across metapopulations. We determined the main effects faced by each metapopulation regarding area sensitivity, population size, intraspecific competition, and disturbance. To enhance the landscape-scale conservation of giant pandas and various other wildlife across China’s national park system, we propose that metapopulation management incorporates population status along with density-dependent and disturbance-related effects on habitat selection.

INTRODUCTION

The giant panda Ailuropoda melanoleuca is a large, territorial mammalian species endemic to southwestern China. It is China’s conservation flagship species and a global icon for nature conservation (1, 2). Over recent decades, the Chinese government has implemented a set of policies and actions to preserve giant pandas, with protected areas as a cornerstone for their conservation. Existing protected areas within giant panda habitats include a mosaic of nature reserves, forest parks, scenic areas, and geological parks (3, 4), although gaps in coverage remain between these sites. Furthermore, designated sites have overlapping jurisdictions, where disparate management risks compromising the effectiveness of protected areas (3, 4). In 2017, the Chinese government launched a pilot project for one of China’s first national parks to fill these coverage gaps and reduce management inconsistencies. This Giant Panda National Park (5) integrated more than 80 preexisting protected areas and covers an area of more than 27,000 km² (6). This was announced at the 15th meeting of the Conference of the Parties to the United Nations Convention on Biological Diversity (COP15) held in China in October 2021, along with the designation of four other national parks in this initial batch (7).

During this pilot phase, many studies have been published regarding how to construct and manage the Giant Panda National Park, with an emphasis on consistent conservation management standards across this vast area, connecting isolated populations and habitats and streamlining enforcement to protect against potentially detrimental activities (4, 6, 8, 9). To achieve these goals, the Chinese government has recently finalized a two-level controlled zoning concept integrating core protection with general control zones (6). However, these zoning schemes have largely been developed and delineated to best accommodate diverse use objectives such as resident development and business alongside conservation, nature education, and recreation, as is the case with many national parks internationally (10, 11). Detailed methods for the cohesive management of giant panda populations and their habitats in this national park remain to be addressed (11).

Establishing feasible methods for managing national parks for the large-scale conservation of a particular species that require relatively large areas of habitat requires careful consideration. Especially challenging is to accommodate the species’ population ecology as it relates to its geographic range, population size or abundance, and habitat selection (12). While the geographic range and population size or abundance of giant pandas have been well documented (13, 14), reports of their fine-scale habitat selection vary across the species’ range, although they typically prefer mid-elevation temperate montane forests with gentle to moderate slopes, large trees, moderate to high bamboo densities, and areas away from human activity [e.g., (15–18); for reviews, see (13, 19, 20)]. Consequently, standardizing giant panda conservation across the extensive Giant Panda National Park presents a major challenge.

One factor is the inconsistent definition of habitat availability across large areas (e.g., reserves and mountains), which could skew results for giant panda habitat selection. Habitat selection can be context dependent, affected by variations in population density and resource availability (21). According to the theory of density-dependent habitat selection, individuals will increase their use of suboptimal or marginal habitat patches as population density and resultant intraspecific competition increases (22, 23), although density-dependent habitat selection has not been thoroughly explored for territorial species (24). This theory would predict that individuals in territorial populations will select habitat according to an ideal-dominant or preemptive habitat distribution, where the best sites will be selected primarily by dominants then, and as population density increases,
newly arriving, juvenile, or subordinate (secondary) individuals will increasingly reside in suboptimal or marginal habitat patches (22, 23). Furthermore, habitat selection is often susceptible to environmental stochasticity and human disturbance, because changes in habitat availability and behavioral responses can arise because of anthropogenic influences, such as infrastructure development (25–27). To our knowledge, no study has yet examined how population density affects giant panda habitat selection at a landscape scale, particularly how interactions between human disturbance and habitat characteristics complicate selection behavior [but see (16, 17, 28–30)]. These complexities need to be addressed explicitly to improve large-scale giant panda conservation under the national park system (4).

Given that the landscapes giant pandas occupy are either naturally heterogeneous or fragmented as a result of human activities (31) and populations that exist at different sites experience a different set of ecological constraints and anthropogenic threats (4, 8), it is vital to approach giant panda conservation from a metapopulation perspective (32). A metapopulation refers to a set of local populations that are spatially separated yet interact at some level in the same general geographical area. Appropriate management at the metapopulation level is important because populations in different areas interact with their local environment differently (e.g., dispersal) (33, 34). In this study, we explored landscape-scale giant panda conservation approaches in a metapopulation context. We used range-wide data from the Fourth National Giant Panda Survey. This is one of the largest-scale survey efforts anywhere in the world that has applied a single, standard protocol to define habitat availability across an extensive landscape range. On the basis of these data, we delineated giant panda metapopulations in Sichuan Province, which comprises more than 70% of the wild giant panda population (17), by geographic range, abundance, and relative density and assessed the extent of human disturbance faced by each metapopulation. We then quantified density-dependent and disturbance-influenced effects on habitat selection. Last, we constructed a conceptual framework where these effects were formulated into schemes for managing metapopulations.

**RESULTS**

**Metapopulation status**

We identified 22 giant panda metapopulations in Sichuan Province. Of the 13 metapopulations included in our analyses, the metapopulation with the greatest geographic range was in Minshan K, followed by Qionglaishan C, Qionglaishan B, Liangshan A, Minshan J, Minshan L, Minshan G, Daxiangling B, Qionglaishan A, Qionglaishan D, Xiaoxiangling B, Liangshan B, and Xiaoxiangling A, the latter six had relatively small ranges (Fig. 1). The relative abundance of giant pandas, based on presence signs, was highest in Minshan K, followed by Minshan J, Qionglaishan B, Qionglaishan C, and Minshan G, and there were fewer signs in other metapopulations (Fig. 1). Consequently, the relative density of giant pandas was highest in Minshan K, followed by Minshan G, Minshan J, Qionglaishan B, and Qionglaishan C, while other populations had fewer than 0.1 signs km⁻² (Fig. 1).

On average, giant pandas occurred at sites 3792.9 m (SD = 2425.9 m) from developed land. The Daxiangling B, Liangshan B, Qionglaishan D, Qionglaishan B, and Liangshan A metapopulations were closer to developed land than other metapopulations (Fig. 1 and fig. S1).

**Interactions between giant panda density and habitat characteristics**

The best-fitting generalized additive model (GAM) showed that the probability that giant pandas occupied a site was greater in metapopulations with higher densities compared with those with lower densities (Fig. 2). The probability of giant panda occurrence was affected by the interactions of panda density with elevation, slope, solar radiation, and bamboo cover (Table 1). There was a significant quadratic relationship between giant panda occurrence and elevation (peaking at mid-elevations), but giant pandas expanded their elevational range with increasing density (Fig. 2A). Giant pandas showed a stronger selection for gentle slopes at lower densities and tended to occur more frequently on steep slopes with increasing density (Fig. 2B). Giant pandas were more likely to select sites with higher solar radiation and greater bamboo cover (with marginal significance; Table 1), and the probability of this selection response increased sharply with increasing density (Fig. 2, C and D).

**Interactions between infrastructure disturbance and habitat characteristics**

The probability that giant pandas occupied a site was greater in sites far from developed land compared with those close to developments (Fig. 3) and influenced by the interactions of distance to developed land with elevation, slope, tree diameter at breast height (DBH), and bamboo cover (Table 1). Although there was a quadratic relationship between giant panda occurrence and elevation (peaking at mid-elevations), giant pandas expanded their elevational range with increasing distance to developed land (Fig. 3A). Giant pandas exhibited a slight preference for steep slopes in proximity to developed land and tended to increasingly select gentle slopes with greater distance to developed land (Fig. 3B). Giant pandas were more likely to select sites with larger tree DBH and higher bamboo cover, but as the distance to developed land increased, the probability of such selection response decreased, while their probability of selecting sites with smaller tree DBH increased (Fig. 3, C and D).

**Conceptual framework and schemes for managing metapopulations**

Given each metapopulation’s status in terms of geographic range, abundance, and relative density, as well as the density-dependent and disturbance-influenced habitat selection, we constructed a conceptual management framework that we broke down into six specific schemes (1a, 1b, 2a, 2b, 3a, and 3b): 1a applies to Minshan K, Minshan G, Minshan J, and Qionglaishan C; 1b applies to Qionglaishan B; 2a applies to Minshan L; 2b applies to Liangshan A; 3a applies to Xiaoxiangling A, Qionglaishan A, and Xiaoxiangling B; and 3b applies to Liangshan B, Daxiangling B, and Qionglaishan D (see details in Fig. 4).

**DISCUSSION**

**Metapopulation status**

This study delineated giant panda metapopulations in terms relevant to their landscape-scale conservation, revealing notable variation in geographic range, relative abundance, and relative density among the metapopulations. The level of infrastructure disturbance faced by the metapopulations varied substantially, affecting giant panda metapopulations according to their distance from developed land. We used these findings to address the fundamental problem
of devising a coherent management plan for giant panda conservation across protected areas within the newly established Giant Panda National Park (4), responsive to our discovery that different metapopulations experienced different suites of ecological constraints and anthropogenic threats.

**Density-dependent and disturbance-related effects on habitat selection**

Our range-wide field data provided evidence for density-dependent habitat selection by giant pandas. We found that the effects of elevation, slope, solar radiation, and bamboo cover on the probability of giant panda occurrence responded nonlinearly to panda density. This suggested a preemptive distribution of individuals across habitats (22), as reported in other large territorial mammals, such as wolves *Canis lupus* (35). As a solitary and territorial forest-dwelling montane mammal, giant pandas generally occupy available sites with a home range of at least 3.9 km² (36), with a minimum total area requirement of 114.7 km² (37). Although range perimeters may overlap, dominant or experienced giant pandas appear to preempt the use of best sites by using scent marking (13, 36, 38) and may be

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**Table 1.** Giant panda metapopulations in Sichuan, China. Map showing the geographic range of metapopulations. The inset table reports relative abundance (i.e., the number of presence signs), relative density, and distance to developed land for the 13 metapopulations included in the analysis, not including nine very small populations, detected by the Fourth National Giant Panda Survey. See also fig. S1.
aggressive toward intruders (38). Hence, we expect that subordinate individuals would be forced to reside in suboptimal habitat patches, and, consequently, the use of suboptimal habitat patches would increase sharply with panda density. Our results indeed corroborated that, in larger populations, many individuals used higher elevations and steeper slopes that incur greater energetic costs (36, 39). While solar radiation is a limiting factor for plant growth, especially bamboo, bamboo growing under higher solar radiation generally has a higher cellulose content, which is less palatable and less nutritious for giant pandas (40). Denser bamboo groves can also be more difficult for giant pandas to traverse (13, 36). Therefore, as population density increased, many individuals appeared to be forced to occupy suboptimal habitat patches subject to intense solar radiation and/or with high bamboo cover.

Environmental changes resulting from human disturbance may reduce habitat suitability and alter a species’ habitat selection responses (25–27). Several previous studies have reported that giant pandas avoid areas where intensive human activities took place and that their distribution and habitat use may shift in response to changes in environmental conditions [e.g., (16, 17, 28–30)]. Nevertheless, these studies did not reveal the mechanism through which human-driven impacts interacted with habitat characteristics to govern how pandas use their environment. We found that the probability of giant panda occurrence expanded from a narrower to a broader band across mid-elevations with increasing distance to developed land. Human activities and infrastructure development, such as agricultural expansion, with the grazing of cattle, sheep, and horses, are most intense and cause most disturbance in valleys, below the bamboo forest zone. Moreover, intensifying yak grazing and gathering herbs such as *Fritillaria* spp. for use in traditional Chinese medicine are also steadily spreading into grasslands above tree line (41). We postulate that these sources of human disturbance risk constricting giant pandas into a narrower elevational band of suitable habitat when in proximity to developed land. Furthermore, we found that giant pandas showed a higher probability of selecting steeper slopes, larger trees, and higher bamboo cover in proximity to developed land. This adoption of steeper slopes may reduce encounters with humans, and the utilization of areas with dense bamboo and large trees may secure access to quality refuges for escape or concealment (15). In summary, given that steeper slopes are energetically costly to inhabit (36, 39) and that denser bamboo impedes movement and offers lower-quality foraging (13, 14), we infer that human-induced

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**Fig. 2. Density-dependent habitat selection by giant pandas.** The probability of giant panda occurrence was generated using the best-fitting GAM, where predictors included elevation (m), slope (°), solar radiation (WH m⁻²), tree cover (%), and bamboo cover (%), fitted as interactions with the relative density of giant pandas (signs km⁻²) and distance to developed land (m). Density-dependent habitat selection was observed with respect to these predictors, as indicated by a steeper concave-down quadratic function (A), a steeper slope (C and D), or switching from a negative to a positive slope (B) with increasing panda density.
Table 1. Summary statistics for the best-fitting GAM predicting the probability of giant panda occurrence. Predictors used in the model included elevation (m), slope (°), solar radiation (WH m⁻²), tree DBH (cm), and bamboo cover (%), fitted as interactions with the relative density of giant pandas (signs km⁻²) and distance to developed land (km).

| Variable                                         | edf   | $\chi^2$ | P    |
|--------------------------------------------------|-------|----------|------|
| Elevation × relative density                     | 4.26  | 109.10   | <0.001|
| Elevation × distance to developed land           | 2.69  | 25.10    | <0.001|
| Slope × relative density                         | 1.00  | 13.74    | <0.001|
| Slope × distance to developed land               | 3.00  | 14.07    | 0.003 |
| Solar radiation × relative density               | 1.01  | 9.87     | 0.002 |
| Tree DBH × distance to developed land            | 2.44  | 8.83     | 0.026 |
| Bamboo cover × relative density                  | 2.31  | 3.50     | 0.138 |
| Bamboo cover × distance to developed land        | 2.63  | 32.67    | <0.001|

Fig. 3. Disturbance-influenced habitat selection by giant pandas. The probability of giant panda occurrence was generated using the best-fitting GAM, where predictors included elevation (m), slope (°), tree DBH (cm), and bamboo cover (%), fitted as interactions with the relative density of giant pandas (signs km⁻²) and distance to developed land (m). Disturbance-influenced habitat selection was observed with respect to these predictors, as indicated by a steeper concave-down quadratic function (A), a shallower slope (D), or switching from a positive to negative slope (B and C) with increasing distance to developed land.
environmental pressures force giant pandas to reside in different and sometimes suboptimal habitat, as reported for various other species (25–27).

**Metapopulation management**

Our results demonstrate the ecological complexity of giant panda habitats and largely reconcile the debate concerning variation in how giant pandas select habitat across extensive spatial scales (20). Simultaneously, our results suggest that previous habitat associations reported for giant pandas, based on smaller-scale data subsets or biased toward information on subordinate individuals, could lead conservation practitioners to misinterpret giant panda preferences. When giant pandas live in proximity to humans, habitat use patterns shift to avoid disturbance and include suboptimal or marginal habitat patches. Furthermore, dominant or experienced individuals preemptively occupy high-quality source habitat, forcing subordinate individuals into low-quality sink habitat (22, 35). Then, the concept of metapopulation management is vital for landscape-scale giant panda conservation and should be the focus of more explicit and quantitative future research. For example, habitat suitability models should be revised to emphasize habitat associations for dominant giant pandas far from human activity, with habitat preferences under those optimal conditions setting the standard for management and restoration efforts.

On the basis of these findings, we outline (Fig. 4) a clear, comprehensive evidence-based conceptual framework involving specific schemes for managing metapopulations as a guide for large-scale giant panda conservation. These schemes share the objectives of increasing carrying capacity, supporting genetic and demographic rescue, and reducing the chance of population isolation. While these schemes share many action points (e.g., habitat quality improvement, prevention of habitat loss and fragmentation, and greater habitat connectivity), each scheme proposes specific priorities matched to population and disturbance status. While the concept of increasing habitat connectivity has gained recognition as a key strategy to protect giant pandas (8, 31, 42), we distinguish here between habitat connectivity and landscape permeability. The former characterizes the capacity of individuals to move between populations or habitat patches within populations to mitigate the extinction risk isolated small populations are vulnerable to. The latter refers to the degree regional landscapes are conducive to the species’ dispersal needs and to sustain ecological processes (43). Increased landscape permeability facilitates emigration from large populations, making them more productive by reducing intraspecific competition while potentially also leading to the genetic and demographic rescue of isolated small populations.

We further recommend some detailed approaches for implementing these management actions (Table 2). For example, habitats
(e.g., large old trees and bamboo stands) should be preserved or enhanced as part of measures to discourage and remedy forest resource extraction (e.g., bamboo shoot collection), agricultural expansion, and livestock grazing (17, 30, 44). Infrastructure construction, such as roads, hydroelectric power stations, mining operations, and tourism operations, should be strictly regulated or prohibited to prevent habitat loss and fragmentation (44). Strategies such as implementing corridors (e.g., building road tunnels and planting bamboo forests) (8, 31, 42) should also be encouraged, particularly to mitigate extinction risk for small, isolated populations. Some specifics should, however, be applied on the basis of the conditions faced by each metapopulation. Corridor construction would connect small populations with large ones for immigration (8, 31, 32) and would facilitate panda movement between fragmented habitat patches within small populations to relieve habitat fragmentation (37, 42). Given the problems smaller, isolated populations face from habitat loss or fragmentation and the risks that these could be exacerbated by climate change (8, 45), corridors could be used to improve between-patch connectivity (37, 42). Simultaneously, restoration of suitable habitats (forests with bamboo stands present) (13) around fragmented patches could be applied to enhance patch size. Alternatively, rescued or captive-bred individuals could be translocated into such small populations; however, this approach still requires more informed evaluation, and pilot releases are needed in an intervention management context (8, 14).

Although further studies regarding the underlying dynamics of metapopulations are needed, our metapopulation management concept, incorporating population status, density dependence, and disturbance effects on habitat selection, offers a novel and robust approach to managing wildlife populations and their habitat over extensive, naturally heterogeneous or fragmented landscapes. Ultimately, we hope that our approach will serve as a reference for wildlife management in other newly established national parks in China, such as the Northeast Tiger and Leopard National Park and the Three-River-Source National Park, and more generally for similar work with other at-risk species around the world.

**MATERIALS AND METHODS**

**Study area**

Giant pandas occupy only a few mountain ranges in China. The mountains of Sichuan Province, including the Minshan Mountains, Qionglai Mountains, Daxiangling Mountains, Xiaoxiangling Mountains, and Liangshan Mountains, are home to more than 70% of the wild population (17). We restricted our study to giant pandas in Sichuan.

**Data collection**

We collated data from the Fourth National Giant Panda Survey, conducted between 2011 and 2013 (41). In this survey, more than 13,600 grid plots of predominantly 1.4 km by 1.4 km were systematically established and investigated within the possible distribution areas of giant pandas in Sichuan. To conduct the survey, observers walked along at least 0.75 km of Z-shaped line transect in each grid plot and identified signs of giant panda presence, such as feces, fur, footprints, and paw marks. Observers recorded the GPS (Global Positioning System) location of each presence indicator (i.e., points used) and set a 20-m by 20-m quadrat centered on this point at which they recorded vegetation variables believed to influence giant panda habitat selection, including tree DBH, tree cover, and bamboo cover. In addition to points where panda presence indicators were found, observers also measured these same vegetation variables in 20-m by 20-m “available point” quadrats established at the start and end of each line transect, as well as at transitions in habitat type, or at 200-m changes in elevation along transects [for more details, see Sichuan Forestry Department (41)].

On the basis of a digital elevation model at 30-m resolution provided by the Geospatial Data Cloud Platform (Computer Network

| Table 2. Recommendations for managing giant panda metapopulations. |
|----------------------------------|----------------------------------|
| **Management action** | **Approach** |
| Improve habitat quality to reduce intraspecific competition and/or increase survival rate and reproductive success | To restore or reclaim habitat to the optimum as selected by dominant individuals far from human activity (e.g., forests with large trees and moderate to high bamboo density or cover; see Results and Discussion), to design artificial dens (51), and to discourage forest resource extraction (e.g., bamboo shoot collection), agricultural expansion, and livestock grazing (17, 30, 44) |
| Increase landscape permeability to facilitate emigration | To conserve areas that provide dispersal opportunity (e.g., bamboo forests in gentle slopes) (32) and/or mitigate barriers (e.g., roads) that impede movement (31, 44) |
| Increase connectivity with large populations to facilitate immigration | To build habitat corridors facilitating movement (e.g., road tunnels and bamboo forests) to connect with large populations (8, 31, 32) |
| Restocking | To translocate rescued or captive-bred giant pandas into a highly suitable area after careful evaluation and pilot releases (8, 14) |
| Prevent habitat loss and fragmentation | To prohibit logging and agricultural expansion and reduce infrastructure construction (e.g., roads, hydropower stations, mining operation, and tourism facilities) (8, 31, 42) that may drive habitat loss and fragmentation |
| Increase patch connectivity within populations | To build habitat corridors facilitating movement (e.g., road tunnels and bamboo stands) between fragmented habitat patches (37, 42) within populations |
| Increase patch size | To strengthen restoration of suitable habitats (forests with bamboo stands present) (13) around fragmented patches (37) within populations |
Identifying metapopulations

We delineated independent giant panda metapopulation boundaries based on data from the Sichuan Forestry Department (41), where giant panda habitat coverage was determined by combining giant panda presence with suitable environmental characteristics, such as elevation, slope, forest cover, vegetation type, and key bamboo species. Within each metapopulation range, subpopulations were defined when separated spatially by rivers, roads, and settlements, although with some habitat still potentially connecting these local subpopulations, permitting limited dispersal. In total, 13 metapopulations were distinguished and used in the subsequent analysis, not including nine very small populations [Fig. 1; for more details, see Sichuan Forestry Department (41)]. For comparison among metapopulations, we used the number of giant panda presence signs as a relative index of abundance, given that these indices generally correlate strongly with actual abundance (4). We also calculated the relative density of giant pandas for each metapopulation by dividing the number of giant panda presence signs by the metapopulation range area and took the mean distance between points used by giant pandas and developed land as a proxy for human disturbance (44).

Habitat selection analysis

To quantify density-dependent and disturbance-influenced habitat selection by giant pandas, we applied a resource selection function, which estimated the probability of species occurrence by integrating habitat variables at used or available points (48). To reduce the possibility of model overfitting, we first thinned the used point dataset by generating a 1120-m buffer around each used point and then selected a point randomly when there was an overlap between buffers (37), based on the minimum home range size of giant pandas (3.9 km²) (36). This procedure was also used to prescreen available points and to exclude points where the buffers overlapped with those of the remaining used points. We also excluded points where observers failed to record some habitat variables. Ultimately, we included 1101 valid used points and 3956 valid available points in subsequent analyses.

We used GAMs with the binomial error distribution and a logit link function to determine complex nonlinear relationships and to evaluate the resource selection function. We included topographic and vegetation variables (i.e., elevation, slope, solar radiation, tree cover, tree DBH, and bamboo cover) as predictors and fitted their interactions with the relative density of metapopulations and with distance to developed land. We implemented the GAMs using the “mgcv” package (49) on R (version 4.0.2) (50). We used restricted maximum likelihood as the method for estimating the smoothing parameter and applied tensor product smooths as the smoothing function when fitting interactions. We determined the basis dimension (k) for each smoothed term by examining the effective degrees of freedom (edf) and partial residual plots but constrained the maximum degree of freedom for smoothers to 2 (k = 3) based on relationships for these variables with giant panda habitat selection reported previously (quadratic, monotonic, and linear) [e.g., (15–18); for reviews, see (13, 19, 20)]. We performed stepwise backward selection using Akaike’s information criterion (AIC) to identify the best-fitting model. We excluded the variable with the highest P-value (P > 0.05) from the model at each step of the selection procedure, until the model with the lowest AIC was produced (table S1).

Design of conceptual framework for metapopulation management

To construct a conceptual framework and specific schemes for landscape-scale giant panda metapopulation conservation management, we determined each metapopulation’s status in terms of geographic range, relative abundance, relative density, and density-dependent habitat selection. This enabled us to establish biological effects such as area sensitivity (37), small population risks (i.e., genetic drift and inbreeding) (42), and intraspecific competition (22, 24), which we classified into three categories: (i) large metapopulations with stronger intraspecific competition for habitat, (ii) small metapopulations with a larger range and weaker intraspecific competition for habitat, and (iii) small metapopulations with a smaller range and weaker intraspecific competition for habitat. Correspondingly, we used our empirical results to decide upon which priority management actions proposed in theory by previous studies should be applied. For large metapopulations with stronger intraspecific competition, this led us to recommend undertaking habitat quality improvements (4, 14) based on the habitat preferences of dominant individuals far from human activity or to promote greater landscape permeability to facilitate emigration (8, 32), thus making source populations more productive by reducing intraspecific competition. In contrast, for small metapopulations with weaker intraspecific competition and regardless of the size of their suitable habitat ranges, we caution that these must be safeguarded primarily from being further divided into more and more isolated small populations by preventing further habitat loss and fragmentation (8, 31, 42). Thereafter, we recommend management actions to support genetic and demographic rescue by improving habitat quality to enhance survival rate and reproductive success (14, 51) and/or by connecting these small metapopulations with larger ones to facilitate immigration (8, 31, 32) or restocking (8, 14). For those with smaller suitable habitat ranges, we further recommend increasing habitat patch connectivity or expanding patch size (37, 42) within populations to reduce the chance of population isolation.

Our management proposal also recommends that actions should be flexible to accommodate those potential effects of infrastructure disturbance faced by each metapopulation. On the basis of distances from developed land, we thus classified the disturbance effects faced by each metapopulation as (a) lower-level infrastructure disturbance, for which we recommend preventing further habitat loss and fragmentation (8, 31, 42), or (b) higher-level infrastructure disturbance, for which we propose that managers take actions to improve habitat quality (4, 14), increase between-patch connectivity, and expand patch size (37, 42). These schemes refer to 1a, 1b, 2a, 2b, 3a, and 3b, respectively (see Fig. 4).
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