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A framework for effective long-term conservation in a changing climate

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A R T I C L E I N F O

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A B S T R A C T

The effectiveness of many existing conservation strategies is at risk of being diminished, as they were designed and/or implemented under the assumption of a stationary rather than a changing climate. Continued support for these strategies could divert resources from alternative strategies that are more sustainable over the long term. We introduce the "longevity of existing conservation strategies" (LECS) decision-support framework for proactively assessing and adaptively managing existing strategies to enhance future conservation capacity. The framework, which is based on the concept of climate change refugia, was applied to two prototype conservation strategies, namely the reintroduction of captive-bred giant pandas into historical geographic ranges and the establishment of the Giant Panda National Park (GPNP). Long-term effectiveness was evaluated based on the potential for *in situ* and *ex situ* refugia for a phenologically-diverse bamboo food supply. Application of the LECS framework, using climate scenarios for 2061–2080 under a high emissions trajectory, suggests that 1) panda reintroduction likely would only serve as a near-term strategy except within the current range and portions of the historical range along the Tibetan Plateau, and 2) proactive management of the GPNP is needed that anticipates potential reductions in a diverse bamboo food supply in the northern GPNP and takes advantage of a projected sustained food supply in the central and southern GPNP. These two applications of the LECS framework highlight that ongoing assessment of the long-term effectiveness of existing strategies needs to become a routine component of conservation practice to reduce climate change maladaptation and misplaced conservation.

1. Introduction

A wide range of conservation strategies, such as protected area designations, hunting/fishing bans, species relocations, and reforestation efforts, are currently in place or are in the process of being implemented at locations around the world (Rands et al., 2010).

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Notwithstanding their present-day effectiveness, these existing strategies, which often target a single or small group of species (Fisichelli et al., 2016; Hannah and Midgley, 2023), run the risk of diminished effectiveness if they are not aligned with the future local or regional climate (Oliver et al., 2016; Rands et al., 2010).

Although the need for "climate-smart" conservation (Hansen et al., 2010) is increasingly emphasized (Buenafe et al., 2023), many existing conservation strategies were designed and/or implemented assuming a stationary rather than a changing climate (Oliver et al., 2016). Any consideration of climate was typically limited to historical climate variability (Magness et al., 2022). This focus on a stationary climate likely reflects a limited awareness of the potential impacts of climate change at the time, in some cases decades ago (Rands et al., 2010), the strategy was implemented. Nonetheless, climate change is also not considered in many recent conservation plans and strategies (Hannah and Midgley, 2023). For instance, it was estimated that nearly half of all recovery plans for species facing extinction in Canada do not include climate change (Naujokaitis-Lewis et al., 2021). Some delay between acknowledging the potential impact of climate change and functionally integrating it into conservation planning can be expected, and climate smart conservation is generally considered a relatively recent development (Wilson et al., 2020). That said, multiple other factors continue to constrain the inclusion of climate change into conservation planning. These include the uncertainty surrounding future climate change, in terms of both the nature of future climates and the impact on individual species and locations (Magness et al., 2022), the challenges of designing innovative and effective conservation strategies for a changing climate (Oliver et al., 2016), limited resources for the planning and design of alternative conservation strategies (Ford et al., 2021), and stakeholder perceptions and valuation of climate smart conservation (Buenafe et al., 2023).

Continuing conservation strategies currently in place without modification for potential climate change or implementing plans that do not consider climate change can lead to maladaptation to climate change. Maladaptation, broadly defined, is an action or process that increases vulnerability or reduces opportunities for successful adaptation to climate change (Juhola and Käyhkö, 2023; Schipper, 2020). Although maladaptation is typically described in the context of a specific climate change adaptation policy (Juhola and Käyhkö, 2023), existing conservation strategies that are unlikely to remain effective in a changing climate can also be considered maladaptive, as they may increase the vulnerability, and hence the extinction risk, of the targeted species (Oliver et al., 2016) and limit adaptive capacity by diverting resources from more efficacious measures (Ruiz-Miranda et al., 2020). Existing conservation strategies may also contribute to "misplaced conservation" (Ford et al., 2021) if their continuation makes safeguarding future biodiversity more difficult.

Given the potential for maladaptation and misplaced conservation, a systematic evaluation of the long-term effectiveness of existing conservation strategies under the lens of climate change is needed to identify strategies that (1) will likely continue to contribute to conservation goals, (2) require modifications to not lock in possible detrimental impacts, (3) are unlikely to remain suitable for the targeted species but may be repurposed for other conservation needs, or (4) should eventually be phased out and replaced with alternative strategies. However, evaluation of conservation strategies is challenging, as outcomes are often only observable beyond the typical time frames for conservation planning (Kapos et al., 2009; Ruiz-Miranda et al., 2020; St-Laurent et al., 2022). Thus, the focus is often on the inputs, implementation, management, and outputs of a strategy, with these indicators acting as proxies for longer term outcomes (Kapos et al., 2009; St-Laurent et al., 2022). One consequence is that exit plans are infrequently incorporated into conservation planning or, if included, are rarely implemented (Ruiz-Miranda et al., 2020). Climate change further confounds the evaluation of conservation strategies, as future climate conditions along with their impacts and time scales are uncertain. Therefore, a proactive, anticipatory, and precautionary decision-support framework that explicitly considers uncertainty is needed to aid in the evaluation of the long-term effectiveness of conservation strategies. Such a framework would contribute to the adaptive management (Williams, 2011) of existing conservation efforts, whereby conservation managers not only assess potential outcomes but also respond adaptively (Ford et al., 2021) to minimize maladaptation to climate change and misplaced conservation.

Our goals are two-fold. First, we propose a decision-support framework for the proactive evaluation and management of existing conservation strategies in a changing climate. Second, to illustrate the framework's usefulness, we assess the potential longevity of two prototype conservation strategies specific to the giant panda (*Ailuropoda melanoleuca*), a global icon of biodiversity conservation (Liu et al., 2016).

2. A decision-support framework for proactive and adaptive conservation management

As argued above, a decision-support framework for evaluating the long-term effectiveness of existing conservation strategies is needed to reduce the risk of maladaptation to climate change and misplaced conservation. Given that the intended application of the framework is to support proactive management that is anticipatory and adaptive, an *ex ante* approach that incorporates projections of future climate and considers the uncertainty surrounding these projections is required. In addition, the framework should be systematic and replicable and allow for ongoing evaluation with frequent updating as new information and assessment methods become available. The spatial focus of the framework should complement that of existing conservation strategies, which are often local or regional in scope. Furthermore, the conservation concepts underlying the framework need to be clearly articulated.

The availability of climate change refugia provides the foundation for our proposed decision-support framework, which we refer to as the "longevity of existing conservation strategies" (LECS) framework. Climate change refugia are broadly defined as locations where environmental conditions for a species or group of species are likely to remain favorable (*in situ* refugia) or become favorable (*ex situ* refugia) under climate change (Ashcroft, 2010; Keppel et al., 2012). These potential biodiversity safe havens (Morelli et al., 2016) are typically defined in terms of climatic suitability (Beaumont et al., 2019; Briscoe et al., 2016) and are increasingly being viewed as tools for climate change adaptation (Morelli et al., 2016), with multiple calls to incorporate refugia into conservation planning (Keppel et al., 2015; Michalak et al., 2018; Stralberg et al., 2020). The LECS decision-support framework builds on these recent developments, in particular the Climate Change Refugia Conservation Cycle proposed by (Morelli et al., 2016) for identifying, prioritizing, and managing climate change refugia.

We argue that not only is the management of climate change refugia of itself a conservation strategy, but that the projected future availability of climate change refugia can be used as a diagnostic tool to assess the long-term effectiveness of a range of conservation strategies and minimize the risk of maladaptation to climate change and misplaced conservation. Our underlying thesis is that existing conservation strategies are unlikely to effectively contribute to future conservation capacity if the locations where they are deployed no longer serve as *in situ* refugia for the targeted species (and/or its food supply), or if the loss of *in situ* refugia is not compensated by a gain in *ex situ* refugia.

As illustrated in Fig. 1, the starting point of the LECS framework is the selection of the conservation strategy for which long-term effectiveness will be evaluated, the targeted species of that strategy, the location(s) where it is implemented, and the future time period of interest (Step 1). The present and future extent of *in situ* and *ex situ* refugia are estimated for the species/location/time period selections from spatial fields of relevant observed and projected climate parameters (Step 2). The projections of future climate refugia, along with the

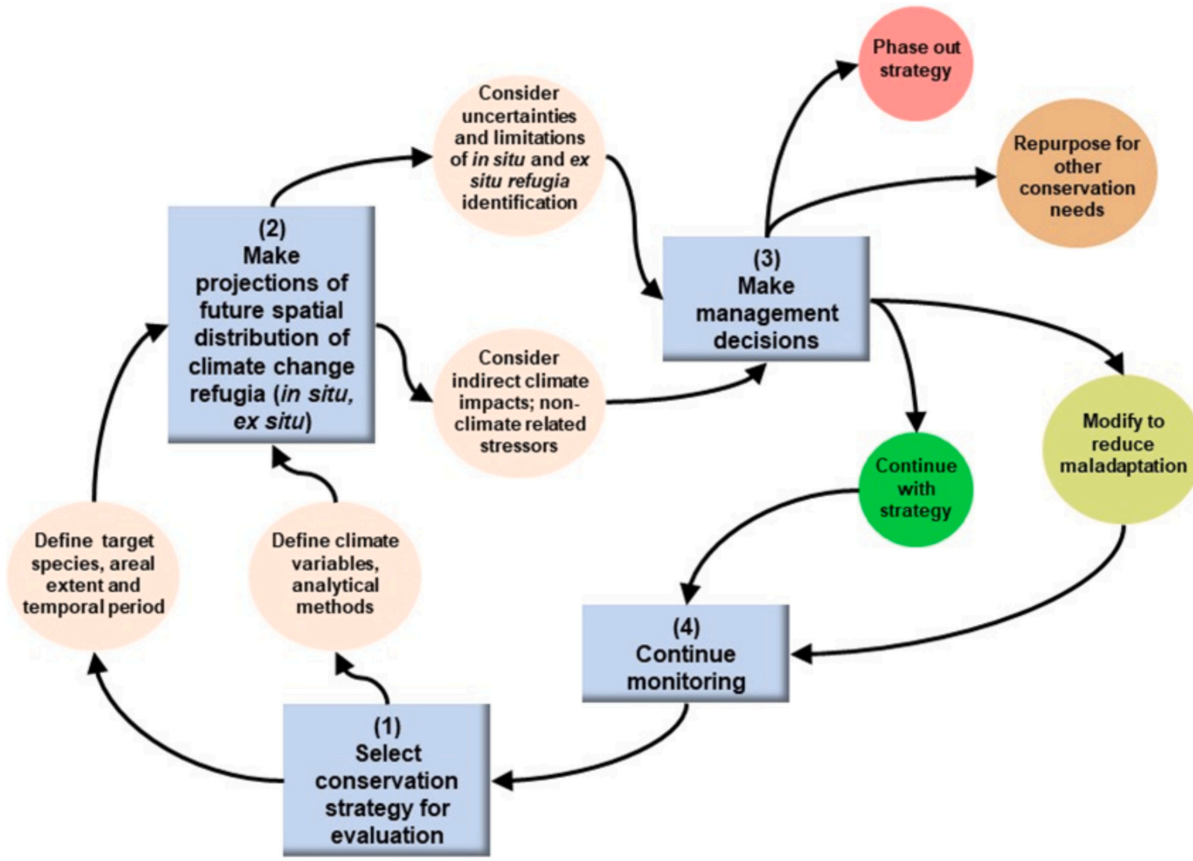

Fig. 1. A decision-support framework for the proactive management of existing conservation strategies under climate change, referred to as the LECS (longevity of existing conservation strategies) framework. The premise underlying the LECS framework is that existing conservation strategies are unlikely to contribute to future conservation capacity if the locations where they are deployed no longer serve as *in situ* climate change refugia for the targeted species and/or its food supply, or if the loss of *in situ* refugia is not compensated by a gain in *ex situ* refugia. The main analytical steps of the framework are shown in blue boxes, with the inputs to these steps and possible decision options shown as multi-colored circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

decision makers' understanding of the uncertainties and limitations of assessing climatic suitability, inform decisions on the long-term management of the selected conservation strategy (Step 3). Ongoing monitoring is another key component of the proposed framework that allows for mid-course adjustments, as the sensitivity of refugia identification to underlying assumptions, data limitations and model specification are better understood, while the "known unknowns" and "unknown unknowns" surrounding future climate change and biological responses to a changing climate are revealed (Smith et al., 2017; Winkler, 2016) (Step 4). The LECS framework can also be expanded to include additional observed and/or anticipated climatic (direct and indirect) and non-climatic stressors. Additional stressors may include, for example, invasive species, pests and diseases, pollution, agricultural expansion, and urban encroachment (Rojas et al., 2022).

The LECS framework accommodates a wide variety of approaches for estimating the location and extent of climate change refugia and the scope of the accompanying uncertainty. For example, climate sensitivity may be represented by a single or a small number of key climate parameters (Rojas et al., 2022) or by multiple climate parameters (Deblauwe et al., 2016), and the methods for estimating refugia locations may range from a graphical overlay and spatial analysis (Rojas et al., 2022) to model simulations such as those from species distribution models (Phillips and Dudík, 2008). Uncertainty estimation may be limited to only uncertainty introduced by the source of future climate projections and the choice of greenhouse gas concentration pathways (Tuanmu et al., 2013) or expanded to also include uncertainty introduced by the limitations of the historical climate data (Tang et al., 2018) and the species observations (Tang et al., 2020) employed in the analysis, together with the modeling techniques (García-Callejas and Araújo, 2016), predictor variables (Petitpierre et al., 2017), and model parameterizations (Boria et al., 2017) selected for estimating climate sensitivity and refugia identification. Numerous approaches can be used to communicate and integrate uncertainty into decision making, ranging from the use of unweighted or weighted ensemble averages (Araújo and New, 2007) to the application of Robust Decision Making (Popper et al., 2005) to "stress test" conservation strategies under a large number of potential future conditions (Rutschmann et al., 2025). Because the LECS framework is meant to encourage longitudinal assessments of the long-term effectiveness of existing conservation strategies, it is essential that whatever methods that are selected are well-documented and assumptions acknowledged to facilitate future updating.

As noted above, the LECS framework was informed by the previously-proposed Climate Change Refugia Conservation Cycle (CCRCC) (Morelli et al., 2016). Climate change refugia are central to both conceptual frameworks, and both emphasize the importance of ongoing evaluation and frequent updating. However, the two frameworks differ in terms of their intent, with the overall goal of the CCRCC to assist adaptation to climate change while that of the LECS framework to minimize maladaptation and misplaced conservation. These differences are highlighted by the initiation points of the two frameworks, with an application of the CCRCC beginning with the identification of conservation goals and a LECS application starting with the selection of a conservation strategy whose longevity is in question. Moreover, the identification and management of climate change refugia is the primary focus of the CCRCC, whereas for the LECS framework the projected existence of climate change refugia serves as a metric for assessing the future longevity of a specified conservation strategy. Importantly, the LECS framework explicitly includes an exit option for those conservation strategies that are unlikely to remain effective in the long term. Two prototype conservation strategies are used below to illustrate potential applications of the LECS decision-support framework.

3. Methods

3.1. Prototype conservation strategies

Giant panda conservation provides a useful case analysis for the evaluation of the LECS framework. Panda populations, although still fragmented, have increased over the past two decades, primarily due to the implementation of conservation strategies such as panda nature reserves, strict enforcement of poaching bans, and national forest conservation policies (Wei et al., 2018). Two recent conservation strategies that build on these earlier efforts are: (1) reintroduction of captive-bred pandas into both their current and former geographic ranges (Hong et al., 2019), and (2) the establishment of the Giant Panda National Park (GPNP), which aims to connect fragmented panda habitats and unify nature reserve jurisdictions (Kang and Li, 2018). Given their importance in ongoing conservation efforts, these two strategies were selected as prototypes for illustrating the utility of the LECS framework.

Since the giant panda is an extreme dietary specialist that almost exclusively feeds on understory bamboo species (Schaller et al., 1985), the long-term effectiveness of these strategies will depend on whether the locations for panda reintroduction will persist as climate change refugia for the bamboo species constituting the panda's staple food supply, and whether the GPNP encompasses *in situ* and *ex situ* climate change refugia for bamboo species. Furthermore, the search for bamboo with the highest nutritional value on a seasonal basis (Li et al., 2017) makes giant pandas elevational migrants, following seasonal patterns that vary across their geographic range (Liu et al., 2015). Consequently, continued phenological diversity of the bamboo food supply is more important than the persistence of a few individual bamboo species. Thus, we used the future availability of *in situ* and *ex situ* climate change refugia for a phenologically-diverse bamboo food supply to assess the long-term effectiveness of the two conservation strategies.

3.2. Modeling approach

While the LECS framework can accommodate a wide variety of methodologies, we employed correlative species distribution modeling, which relates species occurrence to environmental conditions (Halvorsen et al., 2015) and has previously been applied to evaluate climatic suitability and identify potential climate change refugia (Briscoe et al., 2016; Keppel and Wardell-Johnson, 2012). Specifically, we used Maxent, a maximum entropy modeling algorithm that accommodates presence only species occurrence observations (Phillips and Dudík, 2008), to estimate current and projected future climate suitability for a phenologically-diverse bamboo food supply. The large literature on Maxent's assumptions and limitations (Bryn et al., 2021; Čengić et al., 2020; Halvorsen et al., 2015; Merow et al., 2013; Yackulic et al., 2013), along with our previous experience applying Maxent to investigate bamboo distributions in southwest China (Tang et al., 2018; Tang et al., 2020; Tuanmu et al., 2010; Tuanmu et al., 2013), helped to inform model design and anticipate sensitivities and potential biases in model outcomes.

3.3. Study area

The historical range of the giant panda can be divided into its current (Viña et al., 2010) and former ranges, with the latter indicated by fossil records from the late Pleistocene (*ca.* 15,000 years bp) (Hunt, 2004). We used reported boundaries of the historical range (Liu and Viña, 2014; Loucks et al., 2001) slightly extended toward the west to ensure that all 67 of the currently-established giant panda nature reserves were included within the study region. Due to the irregular shape of the historical range, all modeling was performed for the land areas within a larger region, referred to as the "modeling region" (Fig. 2). Modeling outputs were then clipped to (1) the historical range and (2) the reported extent of the GPNP (Holland, 2019). Note that on Fig. 2 and the following figures the map lines delineate study areas but do not necessarily depict accepted national boundaries. The names of provinces and mountain ranges referred to in the text are shown in Fig. 2.

We also considered the locations of nature reserves within the historical range, under the assumption that panda reintroduction is more likely to occur within protected areas. Boundaries of the current panda reserves were obtained from the Shaanxi Forestry Department, and the boundaries of other nature reserves were obtained from (Xu et al., 2017). When boundary information for a particular reserve was unavailable, Xu et al. used a circular area centered around the point location obtained from the Nanjing Institute of Environmental Sciences, with the size reported by China's Ministry of Ecology and Environment.

3.4. Bamboo presence locations

An underlying assumption when applying Maxent is that species presence is well sampled across the study area (Phillips et al., 2009). Sampling bias is a major challenge for species distribution modeling in general (Bryn et al., 2021; Merow et al., 2013; Yackulic et al., 2013) and is a concern here due to the limited availability outside of the current panda range of field observations for the bamboo species that serve as food sources for the giant panda. As the current panda range is located at higher elevations than most of the former range, the relationship between bamboo presence and climate for the historical range may be truncated and the present-day climatic niche poorly defined (Faurby and Araújo, 2018) if presence observations from only the current range are used for model calibration. To address this, we employed time series of the Wide Dynamic Range Vegetation Index (WDRVI) (Gitelson, 2004) together with bamboo field sample locations from the current panda range to derive remotely-sensed estimates of bamboo presence across the historical range, and used the remotely-sensed presence locations to calibrate Maxent. Our procedures expand on prior work (Tang et al., 2020) that used the WDRVI and bamboo field observations to estimate bamboo presence for a study region in southwest China that included both sampled and unsampled areas for bamboo occurrence, finding that the simulated presence locations in the unsampled areas agreed well with bamboo locations from vegetation atlases and other secondary sources.

The estimation of bamboo presence is based on the mismatch between the phenological signatures of overstory canopies with and without an understory of bamboo (Tuanmu et al., 2010; Viña et al., 2008). The WDRVI was calculated from 8-day surface reflectance values in the red and near infrared spectral bands (250 m/pixel) of the Moderate Resolution Imaging Spectroadiometer (MOD09Q) product. [The MOD09Q dataset is available from the Land Processes Distributed Active Archive Center (Vermonte, 2015) at https://www.earthdata.nasa.gov/centers/lp-daac (accessed 30 April 2026).] The WDRVI was preferred over the more commonly used Normalized Difference Vegetation Index (NDVI), as it does not lose sensitivity at the moderate-to-high green biomass conditions characteristic of the forests in the study area (Viña et al., 2008). To reduce the potential effects of temporal autocorrelation, a principal components analysis was applied to the WDRVI image time series (Viña et al., 2010), and 10 components were retained based on the variance explained by the components.

Bamboo field observations for the current panda range were obtained from the Third (2000–2004, hereafter 3S) (State Forestry Administration, 2006) and Fourth (2011–2014, hereafter 4S) (State Forestry Administration, 2015) National Giant Panda Surveys. The 3S

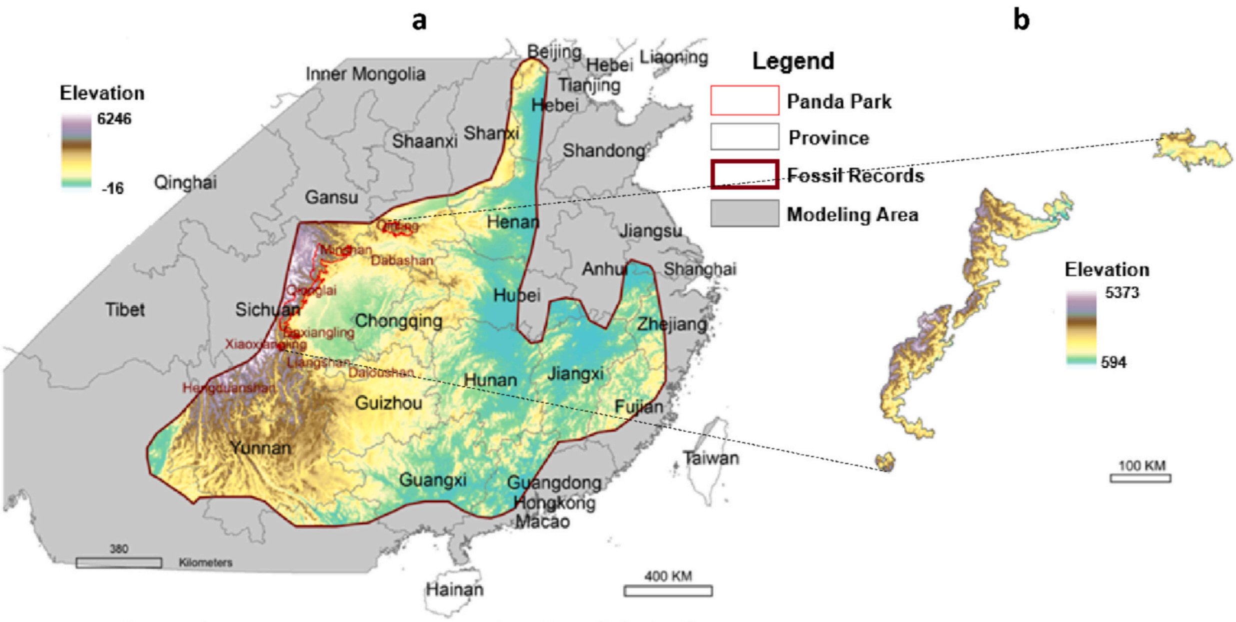

Fig. 2. Study area. (a) Extent of the area used to model climatic suitability for phenologically-driven bamboo groups (shaded in gray), superimposed with a digital elevation model of the giant panda's historical geographic range, and geographical place names. (b) Elevation variations across the Giant Panda National Park.

and 4S covered over 23,000 km^2 and 43,000 km^2, respectively, in the provinces of Sichuan, Shaanxi, and Gansu. [The 3S and 4S field observations are available from the National Forests and Grasslands Administration of China, https://www.forestry.gov.cn/.] Only bamboo species confirmed by the 3S and 4S as food sources for the giant panda were included in the analysis. Species with less than 10 reported occurrences were not considered due to concerns regarding data quality and potential modeling bias, leaving a total of 43 bamboo species and, after duplicate observations and observations with obvious location errors were deleted, 40,074 individual bamboo presence locations (Table S1). While the 3S and 4S were limited to the current panda range, the majority of the 43 bamboo species also occur within the historical range, with their spatial extent varying by species (Fang et al., 2011). Bamboo species that could potentially become food sources in the future were not considered, given the difficulty in projecting future food adaptations by the giant panda.

We first grouped the pooled 3S and 4S bamboo field observations into phenologically-similar groups, as defined using the WDRVI time series, and developed classification algorithms for each group rather than for individual species. This approach assesses bamboo availability and phenology, both of which contribute to a seasonally-continuous food supply for the giant panda. An additional advantage is that, although the utility of remote sensing in identifying bamboo occurrence has previously been demonstrated (Tuanmu et al., 2010; Viña et al., 2008), distinguishing between individual bamboo species is more challenging, as bamboo species may share the same overstory species and/or have similar phenological characteristics (Tuanmu et al., 2010). Furthermore, many bamboo species are physically similar, leading to misidentification errors in field observations, which in turn introduces errors when developing classification algorithms for individual species. Thus, the use of phenologically-similar groupings reduces potential biases due to species misidentification, and, furthermore, the effects of the overstory canopy are minimized, since it has been shown that floristically similar areas (*i.e.*, composed of similar overstory and understory species) will also be phenologically similar (Viña et al., 2016; Viña et al., 2012).

We used k-means cluster analysis to group the pooled 3S and 4S field observations based on the scores of the WDRVI principal components. A drift option was specified to update the cluster seeds every time an observation was reassigned (SAS Institute, 2004). We applied the widely-used elbow method (Everitt, 2010) to select the number of clusters for further analysis. We performed the cluster analysis for all possible numbers of clusters and plotted the within group sum of squares against the number of clusters and searched for a change in slope (*i.e.*, elbow) in the plot. Before finalizing the number of clusters, we compared the suggested nine cluster solution to the 7, 8, 10 and 11 cluster solutions and qualitatively evaluated the impact of the choice of cluster number on the membership and spatial distribution of the different clusters. We also considered the stability of the cluster memberships for multiple k-means runs with different initial seeds. These comparisons supported the nine cluster solution as reasonable. K-means analysis specifying nine clusters was then run 30 separate times starting with different randomly-selected initial seeds, with the most frequently-occurring cluster pattern selected as the global optimum (Jolliffe and Philipp, 2010). The final nine groups represent bamboo field occurrences with the most similar phenological characteristics. The number of field occurrence locations for each bamboo group is provided in Table S2.

For each group, we estimated the probability of bamboo presence for every 250 m pixel within the modeling area, based on the 10 WDRVI principal components and the field occurrence locations. We applied Maxent for this task, separate from its application to estimate climatic suitability, as Maxent has been shown to perform well as a one-class classifier of species occurrence when applied to remotely sensed data (Skowronek et al., 2017). As background data, we used the default option of 10,000 randomly distributed pixels across the panda's historical range, based on previous findings (Čengić et al., 2020) that the number of background points does not strongly impact model performance. We performed a cross-validation analysis in which five replicates were obtained by iteratively splitting randomly into training (70%) and testing (30%) subsets, and the area under the receiver operating characteristic curve (AUC) (Hanley and McNeil, 1982) was calculated for each iteration. Average AUC values ranged from 0.810 to 0.979 for the nine bamboo groups (Table S3).

Since there can potentially be millions of presence locations across the modeling area, we selected 0.5% of the locations (*i.e.*, pixels) exhibiting the highest simulated probabilities from Maxent's logistic output and that were located at least 1.5 km apart. The first criterion ensures that only the estimated bamboo presence locations with the highest confidence are included in the analysis. The second criterion reduces the bias introduced by potential spatial autocorrelation among presence locations (Boria et al., 2014). To interpret the logistic output as occurrence probabilities, we reasonably assume that the sampling and detection probabilities of the bamboo field observations are unrelated to the WDRVI principal components (Yackulic et al., 2013). The spatial distribution of the remotely-sensed occurrences is shown for each bamboo group in Fig. S1.

3.5. Climatic suitability

The temperature and precipitation datasets developed by (Deblauwe et al., 2016) at a 0.05 degree (~6 km/pixel) spatial resolution from the MOD11C3 v. 6.0 land surface temperature product (Wan et al., 2015) and the Climate Hazards Group InfraRed Precipitation with Station data version 2 (CHIRPS v. 2.0) product (Funk et al., 2015) were used to estimate the present-day climatic niche for the nine bamboo groups.. [These datasets are available at https://vdeblauwe.wordpress.com/download/ (accessed on 30 April 2026).] Long-term monthly averages of maximum, minimum, and mean temperature, as well as monthly mean precipitation, were obtained for 2001–2013 (for temperature) and 1981–2013 (for precipitation), and resampled and interpolated to a 1 km^2 spatial resolution. This grid cell size balances the depiction of the highly spatially-varying bamboo distributions and climate conditions in mountainous terrains with the relatively modest (4–7 km^2) annual activity ranges of giant panda individuals (Qing et al., 2016).

The remotely-derived baseline climate datasets were preferred over conventional gridded datasets derived from *in situ* climate station measurements due to the finer spatial resolution (30 m to a few kilometers) of the native measurements of the remotely-sensed climate datasets. Native resolution is particularly an issue for the current panda range where long-term climate stations are separated by ~100–200 km with few stations at high elevations (Tang et al., 2018). Furthermore, the choice of baseline climate information introduced as much uncertainty into Maxent simulations of future climatic suitability for bamboo species in southwest China as the choice of future climate projections, a finding attributed to the inability of conventional gridded datasets to capture steep climatic gradients (Tang et al., 2018).

Climate projections for a future (2061–2080) time slice under the RCP8.5 greenhouse gas concentration trajectory were derived using the delta downscaling method and 17 global climate model (GCM) simulations included in the Coupled Model Intercomparison Project Phase 5 (CMIP5) archive (World Climate Research Programme, 2017) (Table S4). The RCP8.5 emissions trajectory was initially considered a "business as usual" scenario, but recent trends in the energy sector suggest that it may be more appropriately described as an unlikely worst-case scenario (Hausfather and Peters, 2020). We chose the RCP8.5 trajectory for our analyses as more confidence can be placed in the potential longevity of the prototype conservation strategies at those locations that are projected to serve as climate change refugia even under the more extreme conditions of a high emissions scenario. Deltas (*i.e.*, change factors) were calculated using the methods summarized in (Tang et al., 2018). The deltas for precipitation are the relative difference (*i.e.*, ratio) at each 1 km^2 grid point between the projected future average monthly precipitation and the GCM-simulated average monthly precipitation for a historical period, whereas the deltas for average monthly maximum, minimum and mean temperature are the simple differences between the future and historical simulations. The deltas were applied to the remotely-sensed long-term averages of temperature and precipitation to obtain future projections for each 1 km^2 pixel within the modeling area.

The standard suite of 19 bioclimatic variables (Hijmans et al., 2005) was considered as potential input variables in the climatic suitability modeling. The values of these variables were generated from average monthly maximum, minimum, and mean temperature and mean monthly precipitation using the R package, "dismo" (Hijmans et al., 2017). As the bioclimatic variables are highly correlated, a principal components analysis with varimax rotation was used to reduce dimensionality to four orthogonal components. Four bioclimatic variables were selected from those variables with the highest loadings on each component (*i.e.*, mean temperature during the warmest quarter of the year, mean temperature during the coldest quarter of the year, mean precipitation during the wettest quarter of the year, and mean precipitation during the driest quarter of the year). Although other bioclimatic variables also had large loadings, the mean temperature and precipitation during the warmest/coldest and wettest/driest quarters, respectively, were chosen over annual averages, as inspection of the future projections from the 17 GCMs indicated that some GCMs projected seasonally asymmetric changes in temperature and precipitation that could have substantial consequences on future bamboo climatic suitability. Plots of the bioclimatic variables for the surveyed bamboo occurrences within the panda's current range and the remotely-sensed bamboo occurrence locations across the historical range illustrate the much larger range of climatic conditions captured by the remotely-sensed occurrences (Fig. 3).

Maxent was used to estimate the present-day climatic suitability for each of the nine bamboo groups. Five replicates were performed, with 30% of the data iteratively retained for model cross-validation. Average AUC values ranged from 0.701 to 0.914 (Table S5). The Maxent modeling coefficients obtained for each of the nine groups under present-day climatic conditions were then applied to the downscaled future climate projections for 2061–2080. To summarize and facilitate communication of the availability of *in situ* and *ex situ* climate change refugia for a phenologically-diverse bamboo food supply, the simulated probabilities (*i.e.*, Maxent's logistic output) were converted into binary presence layers using the equal test sensitivity and specificity (ESS) threshold selection approach following (Liu et al., 2005). Although Maxent's logistic output is a biased estimate of occurrence probabilities when sampling assumptions are not met (Merow et al., 2013), our use of remotely-sensed bamboo presence locations reduces this bias. The decision to employ a single thresholding procedure was based on our previous analysis of the relative contribution of the choice of thresholding procedures to the uncertainty surrounding Maxent simulations of future climatic suitability for bamboo species in southwest China (Tang et al., 2020). Uncertainty estimates obtained from the choice of thresholding options available in Maxent (*e.g.*, Fixed Cumulative Value, Minimum Training Presence, 10 Percentile Training Presence, Equal Training Sensitivity and Specificity, Equal Test Sensitivity and Specificity, Maximum Training Sensitivity Plus Specificity) were found to be smaller than the uncertainty introduced by the choices of presence data and future climate projections. Given this finding, and to make the analysis more tractable, we selected the ESS threshold approach based on its suitability for presence-only modeling (Liu et al., 2005), although other threshold procedures would also be appropriate.

For each of the 1 km^2 pixels within the historical range, the number of bamboo groups exceeding their respective ESS threshold was found for the present-day and future periods, with a larger number of groups per pixel indicating greater phenological diversity. For the future period, a grid cell was climatically suitable for a particular bamboo group if $\geq$9 GCMs, $\geq$12 GCMs, $\geq$15 GCMs, or all 17 GCMs were in agreement. The four criteria provide an indication of the uncertainty associated with the future projections. Next, each 1 km^2 pixel was classified for $\geq$1, $\geq$3 and $\geq$ 5 bamboo groups as (1) climatically suitable for both the present-day and future periods, (2) currently climatically suitable but projected to be unsuitable in the future, (3) projected to be climatically suitable in the future but not currently climatically suitable, and (4) climatically unsuitable in both the present-day and future periods. The three thresholds were selected *via* inspection of the estimated present-day phenological diversity at the locations of the largest panda densities in the Minshan and Qinling Mountains (Tian et al., 2019). The use of multiple thresholds allows for uncertainty in the estimates of present-day bamboo

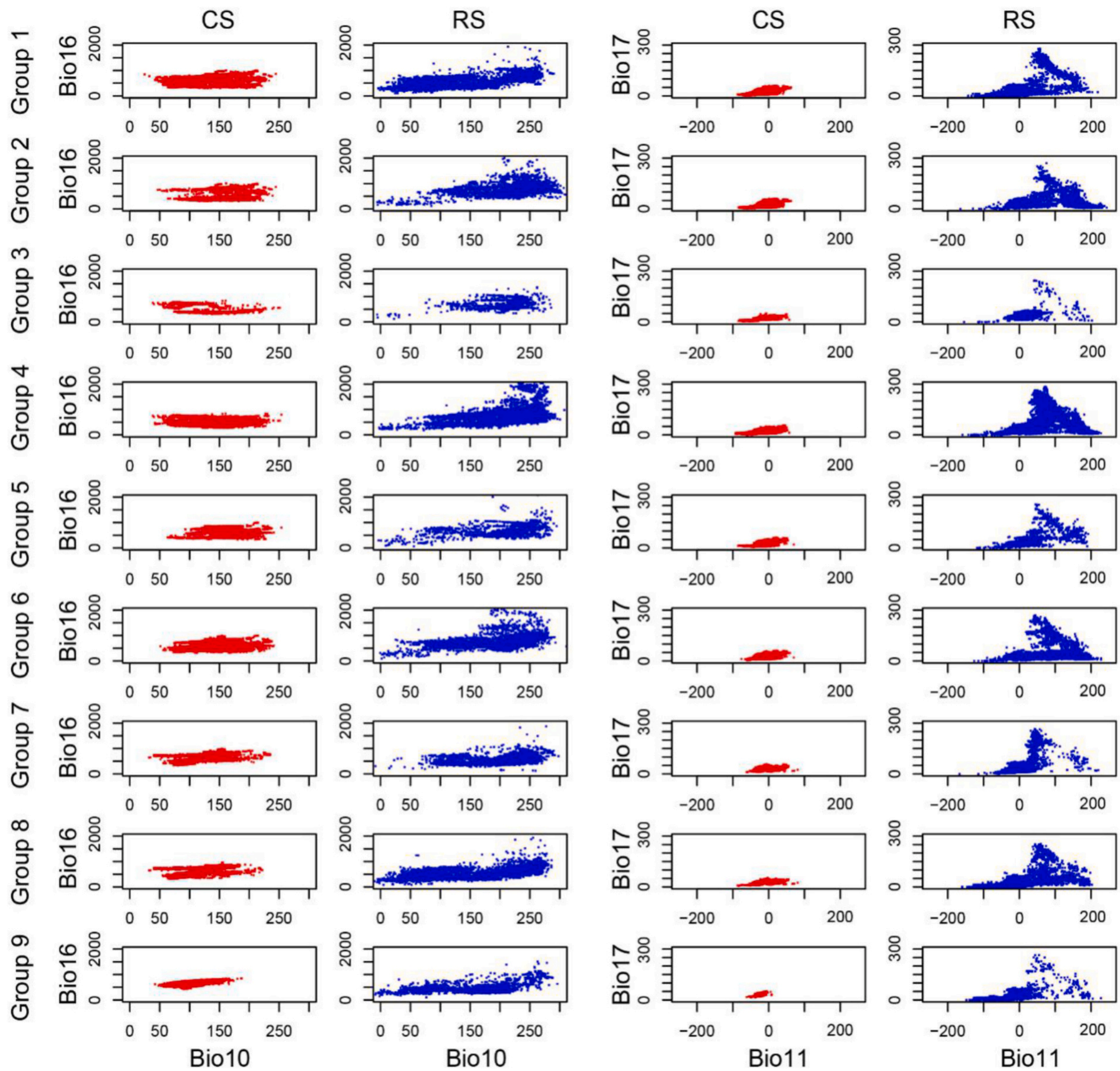

Fig. 3. Environmental conditions for the surveyed bamboo occurrence locations within the current giant panda geographic range (CS; red) and the remotely-sensed bamboo occurrence locations across the giant panda historical geographic range (RS; blue). The environmental conditions are defined in terms of the four bioclimatic variables used in the species distribution modeling. For the left two columns of plots, the horizontal axis is the long-term mean temperature of the warmest quarter of the year (Bio10) and the vertical axis is the long-term mean precipitation of the wettest quarter (Bio16) (units are °C and mm, with both parameters multiplied by 10). As the current and historical panda range experiences a continental climate with typically the highest precipitation coinciding with the warmest temperatures, the two columns on the left can be considered the environmental conditions during "summer". The environmental variables displayed in the two columns on the right are the long-term mean temperature during the coldest quarter (horizontal axis; Bio11) and the long-term mean precipitation during the driest quarter (vertical axis; Bio17), both multiplied by 10. These plots can be considered "winter". (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

phenological diversity and for differences in phenological diversity between present-day panda habitat areas. To assess the change in the climatically suitable area for each nature reserve within the panda's historical range, we calculated the number of 1 km^2 pixels with climatically suitable conditions for (1) at least one bamboo group and (2) at least three bamboo groups for the present-day and future periods, stipulating for the future period that nine or more GCMs were in agreement. The relative change in climatically suitable area, expressed as a percent, was defined as the ratio of the difference in climatically suitable area between the future and present-day periods to the present-day climatically suitable area. We did not consider future impacts of human activities, which may further restrict the habitat selection (Hull et al., 2014) and dispersal ability (Connor et al., 2016) of giant pandas. Also, we assumed unlimited bamboo dispersal ability; consequently, the extent of *ex situ* climate change refugia may be overestimated, as many bamboo species have limited seed and vegetative dispersal abilities (Taylor et al., 1991).

4. Results and discussion

4.1. Projected in situ and ex situ climate change refugia

Present-day climatic conditions are suitable over much of the panda's historical range for at least one of the nine phenologically-driven bamboo groups (Fig. 4). As context, a phenological diversity of three or more bamboo groups per km^2 is found in the Minshan and Qinling Mountains of the current panda range, where population densities are the highest (Tian et al., 2019). Using this value as a guide, climate

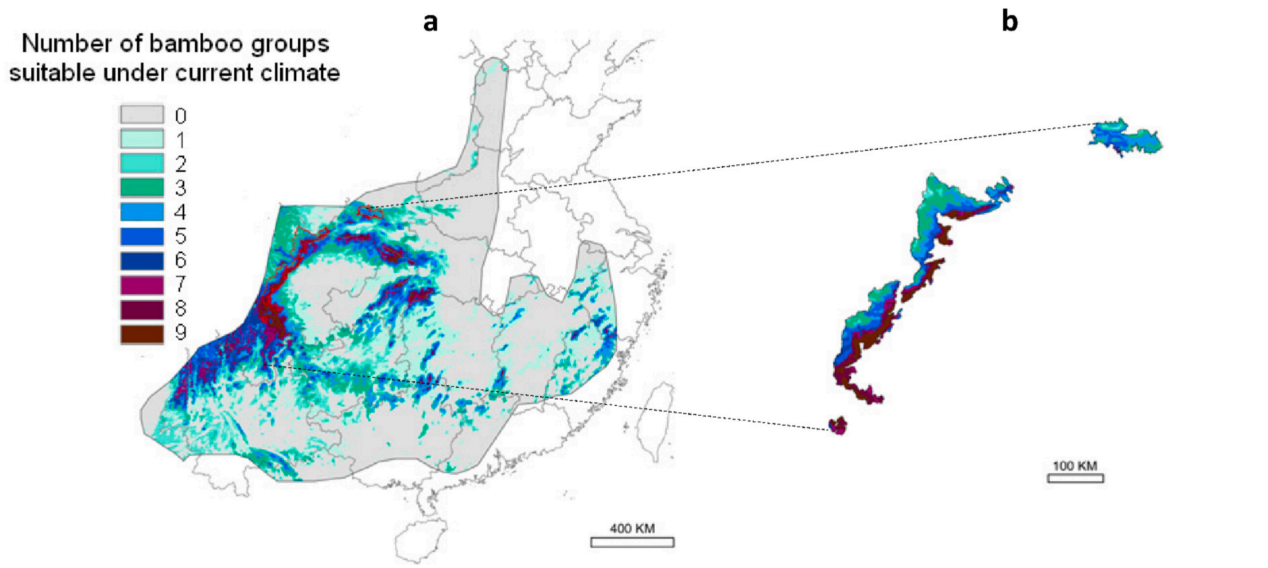

Fig. 4. Present-day climatic suitability for nine phenologically-driven bamboo groups. (a) Number of bamboo groups per km^2 under present-day (1981–2013) suitable climate conditions throughout the historical giant panda geographic range. (b) Number of bamboo groups per km^2 under present-day suitable climate conditions within the Giant Panda National Park.

conditions that are currently favorable for a seasonally available panda food supply extend from the mountainous regions of western Yunnan and Sichuan Provinces to as far east as the mountains of western Zhejiang and Fujian Provinces. Within the GPNP, the highest phenological diversity (*i.e.*, 7–9 bamboo groups) is found along the eastern slopes of the Minshan, Qionglai, Daxiangling, and Xiaoxiangling

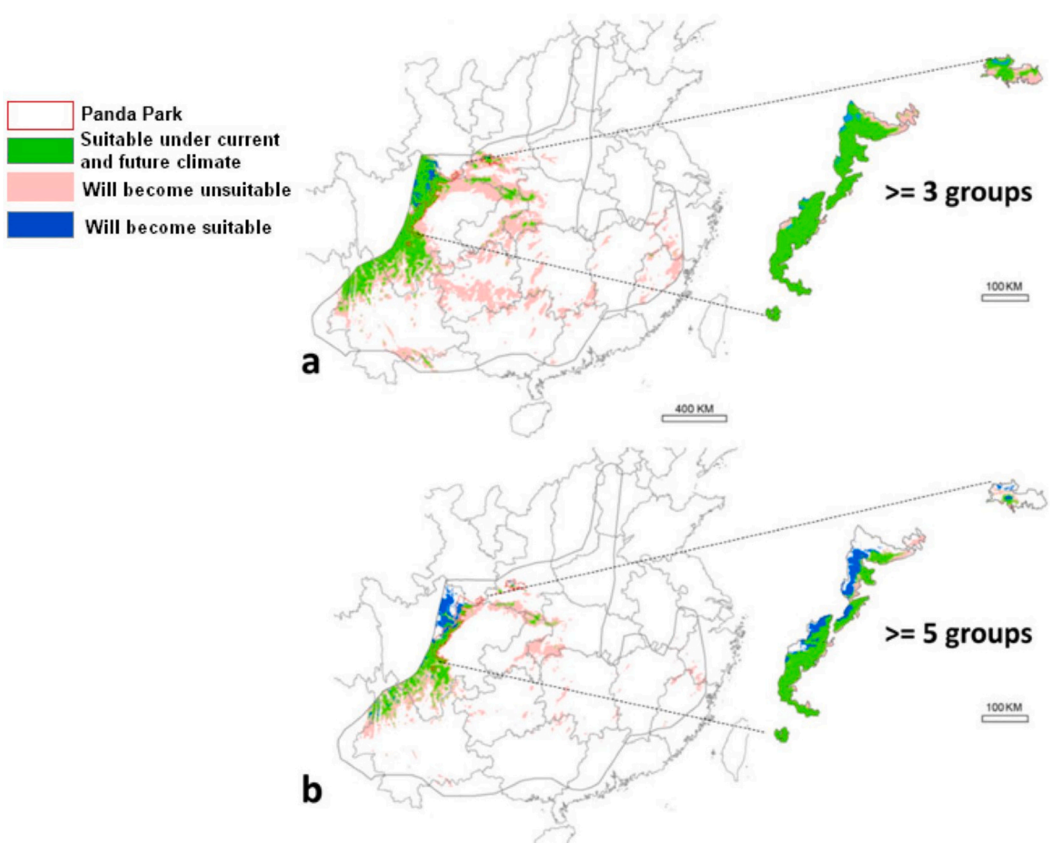

Fig. 5. Projected change between present (1981–2013) and future (2061–2080) periods in climatically suitable conditions within the giant panda historical range and the Giant Panda National Park (insets) for (a) three or more and (b) five or more phenologically-driven bamboo groups. Pixels (1 km^2) that are climatically suitable under present climate conditions but are projected to be no longer suitable by 2061–2080 under the RCP8.5 greenhouse gas concentration trajectory are shown in pink; pixels that are projected to remain suitable are shown in green; and pixels that are not currently suitable but are projected to become suitable are shown in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Mountains, with somewhat smaller diversity (*i.e.*, 3–6 groups) along the southern slopes of the Qinling Mountains (Fig. 4).

In contrast, future climatic suitability for a phenologically-diverse food supply is constrained primarily to the current panda range. This result is based on the persistence of at least three, or at least five, bamboo groups, and under the criterion of more than 50% agreement among 17 global climate model (GCM) simulations for the period 2061–2080 under the RCP8.5 greenhouse gas concentration trajectory (Fig. 5). Harsher criteria (*i.e.*, agreement among 12, 15, and 17 GCMs) result in only modest differences in interpretation (Fig. S2). Notable exceptions within the current range are the Qinling Mountains and northern Minshan Mountains, where some locations are projected to have fewer than three phenological bamboo groups by 2061–2080. Those locations shown in Fig. 5 as suitable for ≥3 and ≥ 5 bamboo groups under current and future conditions (green shading) represent *in situ* climate change refugia, whereas those shown as becoming suitable in the future (blue shading) reflect *ex situ* refugia. Projected *ex situ* refugia are predominantly located at higher elevations within and to the northwest of the GPNP and constitute a larger portion of the climatically suitable area when the harsher criterion of ≥5 bamboo groups is considered. The location and extent of these *ex situ* refugia need to be interpreted carefully, given our assumption of unlimited bamboo dispersal. These areas may not be refugia for a phenologically-diverse food supply if bamboo dispersal is constrained, although, as shown in Fig. 6, they are projected to remain *in situ* refugia for at least one bamboo group. In contrast, the mountain regions west, southwest and south of the current panda range are anticipated to remain as *in situ* climate change refugia for a phenologically-diverse food supply (Fig. 5). However, these areas are projected to experience decreases in the overall number of phenologically-driven bamboo groups, in contrast to projected increases in phenological diversity under unlimited bamboo dispersal in the higher elevation regions within the current range (Fig. 6). Elsewhere across the historical range, except for a few isolated areas with higher elevations, climate conditions are projected to become unfavorable for all phenological bamboo groups evaluated.

4.2. Implications for long-term effectiveness of the prototype conservation strategies

The implications of these projected changes under the RCP8.5 emissions trajectory in *in situ* and *ex situ* climate change refugia for the long-term effectiveness of the two conservation strategies under

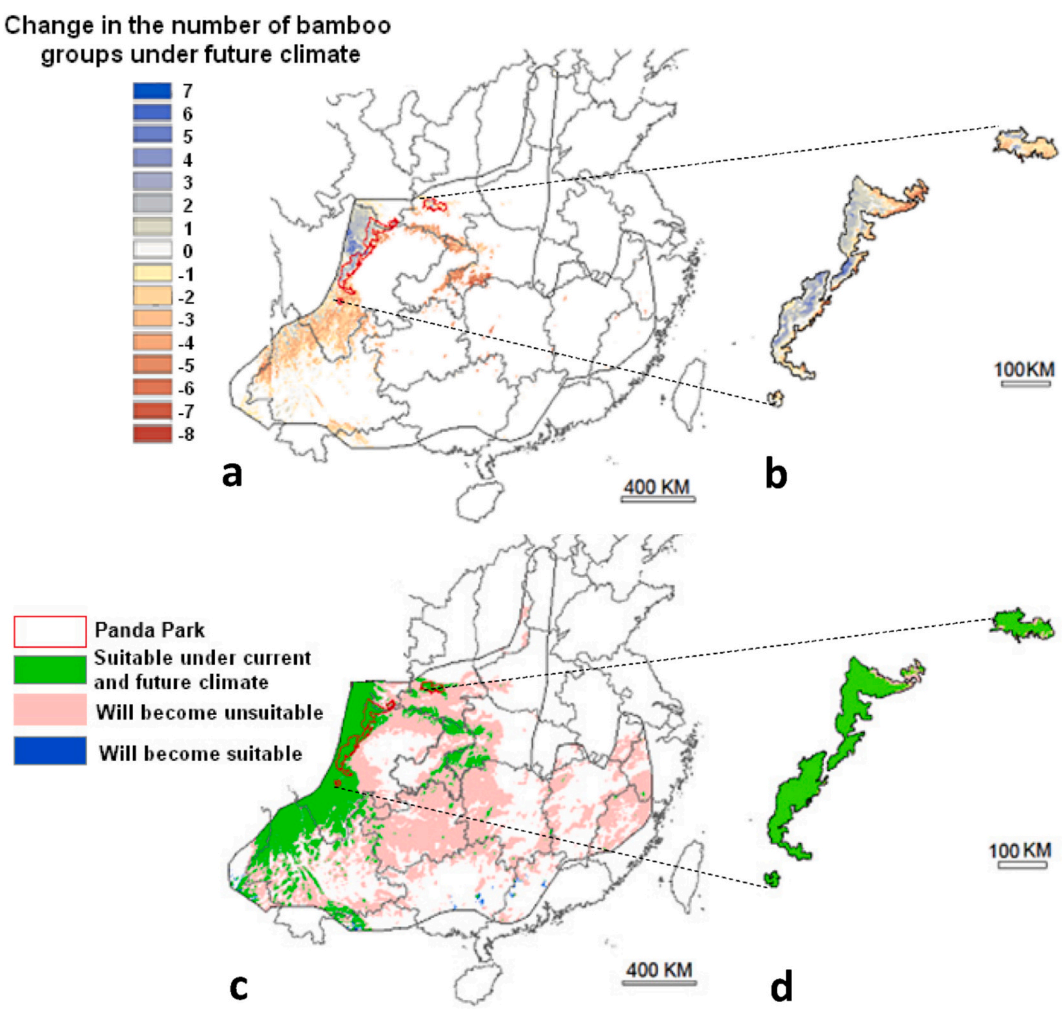

Fig. 6. Projected gains and losses between the present (1981–2013) and the future (2061–2080) periods in the number of phenologically-driven bamboo groups with climatically suitable conditions for (a) the historical geographic range of the giant panda and (b) the Giant Panda National Park, calculated for those pixels (1 km^2) with projected future climatic suitability for at least one bamboo group as shown in green and blue shading in (c) for the historical geographical range and (d) for the Giant Panda National Park. Pixels in (c,d) that are climatically suitable under present climate conditions for at least one bamboo group but are projected to be no longer suitable by 2061–2080 2080 under the RCP8.5 greenhouse gas concentration trajectory are shown in pink; pixels projected to remain suitable are shown in green; and pixels not currently suitable but are projected to become suitable are shown in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

consideration are substantial. If we assume that panda reintroduction is more feasible in established nature reserves, we find that reintroduction is more likely to be successful in the long run only for nature reserves located within the current geographic range and within limited portions of the former range along the Tibetan Plateau, as these reserves are projected to experience only small (<20%) losses, or a slight increase, of phenologically-diverse bamboo habitat by 2061–2080 (Fig. 7). Elsewhere, projected habitat loss within established reserves ranges from 40 to 50% in the Dabashan and Daiashan Mountains to over 80% in the eastern portions of the historical panda range. Thus, reintroducing giant pandas into these reserves likely would only serve as a near-term strategy, while in the long term could reduce conservation capacity. These findings are of particular concern for several proposed reintroduction sites, such as the Huayingshan, Shenlongjia, and Anji Mountains in Sichuan, Hubei, and Zhejiang Provinces, respectively (Hong et al., 2019).

The projected changes in climate change refugia for a phenologically-diverse bamboo food supply also highlight the need for proactive monitoring and management of the GPNP. Persistent *in situ* refugia are most likely in the south central and southern GPNP, which lie largely outside of existing panda nature reserves and currently have smaller panda populations (Xu et al., 2019). The development of corridors for southward panda migration and reintroduction of pandas into the southern portions of the GPNP are possible avenues to take advantage of the expected *in situ* refugia in this area. In the north central and central portions of the GPNP, long-term effective conservation should consider both *in situ* and *ex situ* refugia. At low elevations, it is projected that bamboo phenological diversity will decrease to fewer than five, and in some cases fewer than three, phenological bamboo groups per km^2. At higher elevations this diversity is projected to increase, suggesting that focusing on reducing human disturbance at mid- to high-elevation areas could induce a sustained contribution of the GPNP to panda conservation. However, the projected *ex situ* refugia at higher elevations are dependent on bamboo dispersal, and limited dispersal would constrain their contribution to panda conservation. Long-term management is most challenging for the northern GPNP (comprising the Qinling Mountains), where over 18% of the current panda population resides (Tian et al., 2019). The relatively smaller initial phenological bamboo diversity, coupled with generally lower elevations, contributes to a higher vulnerability of this region. While *in situ* climate change refugia are projected to persist at higher elevations, the total area encompassed within these refugia is projected to be considerably smaller than the present-day climatically suitable area, requiring close monitoring of panda population densities and carrying capacity.

4.3. Management options

To highlight the utility of the refugia-centered LECS framework for proactive decision making and to illustrate possible initial management options for giant panda conservation that are congruent with the climatic suitability analyses, we overlaid the steps and outcomes for each of the two prototype conservation strategies on the proposed LECS framework (Fig. 8). As for any application of the LECS framework, outcomes must be interpreted in the context of the choices made when applying the framework and the underlying uncertainties. With these considerations in mind, possible management options to avoid climate change maladaptation associated with giant panda reintroductions include focusing in the near term on reintroductions within the current panda range and nearby locations along the Tibetan Plateau. In these areas, climatic conditions for a phenologically-diverse bamboo food supply are projected, under a high forcing emissions scenario, to remain suitable well into the future. Elsewhere in the historical range, it may be more appropriate to postpone reintroductions until key uncertainties, such as future emissions trajectories, bamboo dispersal rates, and

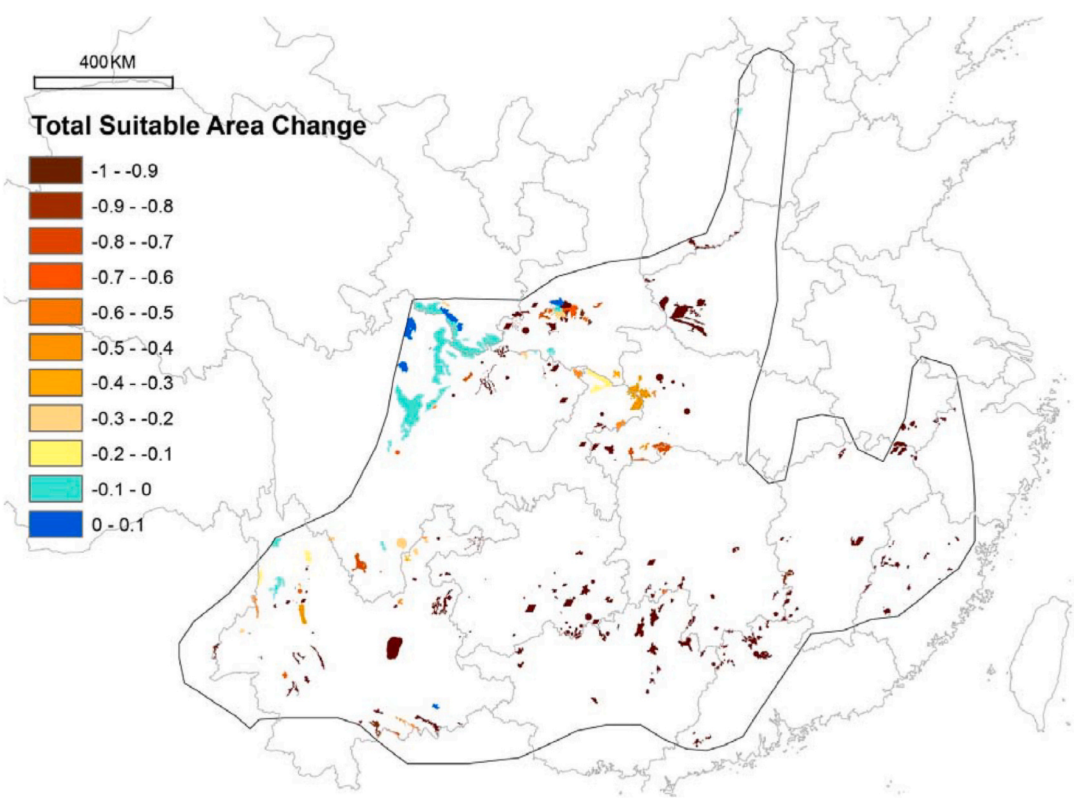

Fig. 7. Proportional change projected for 2061–2080 under the RCP8.5 greenhouse gas concentration trajectory in the area within currently established nature reserves located throughout the historical giant panda geographic range that is climatically suitable for three or more phenologically-driven bamboo groups. Warm colors indicate losses, whereas cool colors represent increases, in climatically suitable area. Percent changes can be found by multiplying the proportional changes by 100.

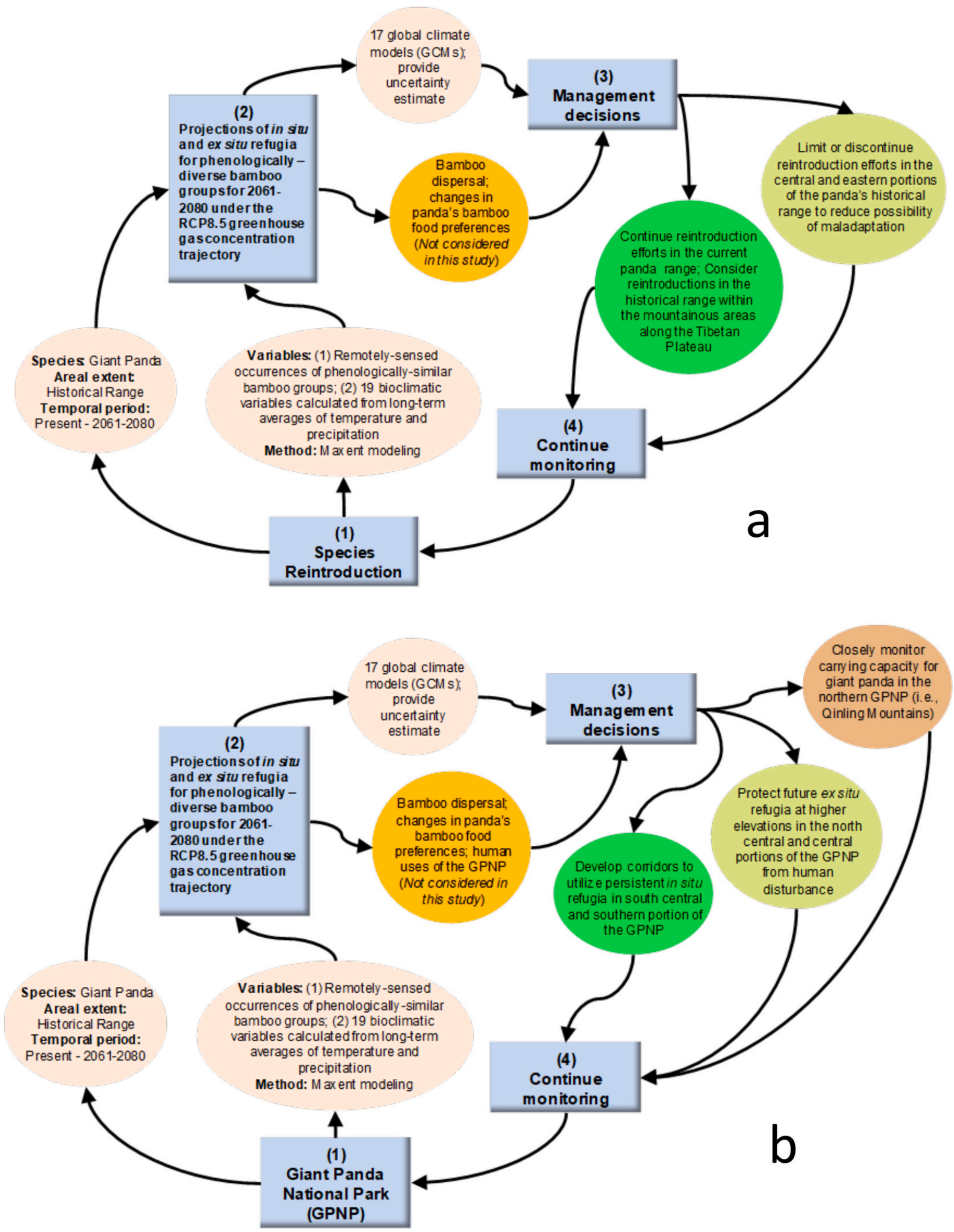

Fig. 8. Application of the LECS decision-support framework for the proactive management under climate change of two prototype conservation strategies. (a) The framework applied to giant panda reintroductions. (b) The framework applied to the Giant Panda National Park (GPNP). The main analytical steps are shown in the blue boxes, with the inputs to these steps, uncertainties and/or stressors not included in the assessment, and decision options shown as multi-colored ovals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

possible changes in the panda's bamboo food preferences, are better understood. The decision-support diagram for the GPNP illustrates that the challenges for its long-term management include anticipating potential reductions in a phenologically-diverse bamboo food supply in the northern portions of the GPNP where panda populations are currently large while simultaneously taking advantage of the projected sustained phenologically-diverse food supply in the southern portions of the GPNP where panda densities are currently low. Moreover, careful consideration and thoughtful management are needed for locations which are unlikely to be suitable in the long-term for a diverse bamboo food supply, but which may serve as intermediate “stepping stones” in a changing climate (D'Aloia et al., 2019). The diagrams shown in Fig. 8 also highlight the importance of ongoing monitoring and mid-course adjustments along with the consideration of additional stressors such as human pressures on bamboo availability and on the giant panda itself.

4.4. Limitations and opportunities

The application of the LECS framework requires numerous decisions on the part of the analyst. Some of these decisions reflect the goals of the longevity assessment, the characteristics of the conservation strategy under investigation, and the locations where the strategy is implemented, whereas other choices are made to increase the tractability of the assessment and address data and analytical limitations and uncertainties. These decisions impact the outcomes of the LECS framework and highlight the need for ongoing reiteration of the assessment process as the sensitivity of the longevity assessment to these choices is better understood.

Several choices affect the outcomes of the longevity assessments for the two prototype conservation strategies evaluated here. One such choice is our decision to include a single emissions scenario, the RCP8.5 greenhouse gas concentration trajectory. As noted earlier, we chose this emissions trajectory since more confidence can be placed in the potential longevity of the prototype conservation strategies at locations that are projected to serve as climate change refugia even under the more extreme conditions of a high emissions scenario. A consequence of this choice is that the projected changes in climatic suitability may be overly pessimistic compared to projections from alternative, lower emissions trajectories. Some previous studies for individual bamboo species support this contention. For example, it was estimated that by the 2070s the colonized area for *Bashania fargesii* in the Qinling Mountains would decrease by 68% under the moderate RCP4.5 emissions trajectory compared to 84% under the RCP8.5 trajectory (Zhao et al., 2023). On the other hand, the analysis by Tuanmu et al., also for the Qinling Mountains, suggested that projected reductions in the area of giant panda habitat based on the climatic suitability for three bamboo species (*Fargesia qinlingensis*, *Fargesia dracocephala*, and *Bashania fargesii*) and three future time slices was similar for high (SRES A2) and moderate (SRES B2) emissions trajectories but varied substantially by GCM (Tuanmu et al., 2013). Similarly, current panda reserves were projected under three RCPs (2.6, 4.5, 8.5) to no longer be climatically suitable by 2070 for six of twelve bamboo species studied (Li et al., 2015). We conclude that projected changes in climatic suitability for the prototype conservation strategies evaluated here are likely smaller, but still substantial, for moderate emissions trajectories. Our analyses would also benefit from the inclusion of multiple future time slices to assess the temporal evolution of changes in climatic suitability.

Another limitation is the assumption of unlimited bamboo dispersal ability as this may contribute to the overestimation of *ex situ* refugia. This is particularly a concern for the longevity assessment of the GPNP, as higher elevations within the northern portions of the GPNP are projected to become climatically suitable for a phenologically-diverse bamboo food supply while phenological diversity is expected to decrease at lower elevations. If bamboo fails to disperse to these higher elevation locations, the projected *ex situ* refugia will not become food sources for the giant panda, and a phenologically-diverse bamboo food supply will be constrained to a smaller geographic area. Incorporating dispersal into climatic suitability modeling is challenging, as SDMs such as Maxent assume either no dispersal or unlimited dispersal, although several recent studies have attempted to integrate dispersal models into SDMs (Duan et al., 2026).

Our longevity assessments also did not address the potential impact of human activities, which can place additional pressure on climate change refugia and impact the longevity of conservation strategies. Human activities are a concern for both prototype strategies evaluated, as population pressure at lower elevations and the upward expansion of human activities (Hull et al., 2014) limits panda reintroduction locations and can contribute to fragmentation of the bamboo food supply within the GPNP. Evaluating the impact of human activities on climate change refugia is notoriously difficult, as it involves identifying appropriate parameters that capture the range of human impacts and projecting the future change in these parameters (Frans and Liu, 2024).

Consideration of "known unknowns" in the longevity assessments of the prototype strategies was also limited. Of particular concern are infrequent, often once in decades, mass flowering events when bamboo synchronously flowers over large areas and subsequently die-off, with recovery of bamboo forests occurring over several years (Tian et al., 2019). In addition, bamboo is vulnerable to fungal pathogens that reduce their nutritional value (Wajid et al., 2026). Therefore, mass flowering events and fungal diseases reduce the availability of a phenologically-diverse food supply for the giant panda. Moreover, their frequency and severity may be affected by climate change (Wajid et al., 2026), compounding their influence on the longevity of the prototype conservation strategies.

Although there are numerous challenges, the LECS framework provides a structure for exploring the longevity of conservation strategies and the potential for maladaptation and misplaced conservation. A particular strength of this framework is that it allows the operationalization of a wide range of methods. For instance, an assessment of the longevity of conservation strategies for a target species with a more complex food web than the giant panda could directly model the climatic suitability of the target species rather than that of its food supply, assuming that appropriate occurrence observations are available. If a conservation strategy is oriented toward a community rather than a single species, climatic suitability and projected presence locations obtained from single species models for each of the keystone species in the community could be composited to obtain the projected climatic suitability for the community. Alternatively, SDM models that consider communities and biotic interactions, such as joint species distribution models (JSDMs), could be used, although data requirements, assumptions, and computational requirements substantially increase with these model types (Pollock et al., 2014). If the conservation strategy is not species-specific (*e.g.*, habitat restoration), one option is to apply the domains of refugia approach (Rojas et al., 2022), which uses a graphical overlay and spatial analysis to assess refugial capacity based on the level of exposure to multiple pre-defined stressors. These examples highlight the many opportunities for investigating the longevity of conservation strategies using the LECS framework.

5. Conclusions

The two prototype conservation strategies evaluated here highlight the value of explicitly assessing the potential long-term effectiveness of current and ongoing conservation strategies under a changing climate. For both, careful management will be needed so that these efforts continue to contribute to increased conservation capacity for the giant panda and to guard against maladaptation to climate change and misplaced conservation. Moreover, the analyses illustrate the potential utility of the proposed refugia-based LECS framework for assessing the long-term effectiveness of conservation strategies. Although the significance of *in situ* and *ex situ* climate change refugia in conservation planning is increasingly being recognized, the emphasis of prior work has been on the habitat preservation of anticipated climate change refugia. In other words, the focus to date has been on refugia as an adaptation strategy. Instead, we use the anticipated existence of climate change refugia as a tool for diagnosing the potential long-term effectiveness of a selected conservation strategy with the intent of minimizing the possibility that the selected strategy contributes to climate change maladaptation and misplaced conservation.

The LECS framework described here offers a potential approach to address the urgent need for systematic assessments of the long-term effectiveness of current conservation strategies. With further testing across different contexts and species, it can assist managers to harness conservation efforts to enhance future conservation capacity, minimize maladaptation to climate change and misplaced conservation, and ensure the longevity of conservation success stories, such as that of the giant panda.

CRediT authorship contribution statement

Ying Tang: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Conceptualization. **Julie A. Winkler:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization. **Andrés Viña:** Writing – review & editing, Visualization, Supervision, Methodology, Funding acquisition, Conceptualization. **Fang Wang:** Writing – review & editing, Methodology. **Veronica F. Frans:** Writing – review & editing, Methodology. **Jindong Zhang:** Writing – review & editing, Methodology. **Zhiqiang Zhao:** Writing – review & editing, Methodology. **Thomas Connor:** Writing – review & editing, Methodology. **Hongbo Yang:** Writing – review & editing, Methodology. **Yuanbin Zhang:** Writing – review & editing, Resources, Methodology. **Xiaofeng Zhang:** Writing – review & editing, Resources, Methodology. **Xiaohong Li:** Writing – review & editing, Resources, Methodology. **Weihua Xu:** Writing – review & editing, Methodology. **Zhiyun Ouyang:** Writing – review & editing, Methodology. **Jianguo Liu:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2026.115065.

Data availability

Data will be made available on request.

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