

Hidden roles of protected areas in the conservation of biodiversity and ecosystem services

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Abstract. Many of the current protected areas worldwide are established for the conservation of particular species of interest, yet their benefits may go beyond these species since they could also contribute to the conservation of entire biodiversity pools. In addition, they may also contribute to the provision of ecosystem services. However, these benefits are seldom evaluated or targeted for improvement. Using field and remotely sensed data, we evaluated how representative of the plant biodiversity pool and of carbon sequestration is a network of nature reserves specifically established for the conservation of a target species, the giant panda (*Ailuropoda melanoleuca*), an icon of biodiversity conservation. Our results show that forest structure (including tree/bamboo species composition) within the nature reserve network is representative of the forest structure across the entire study region, with the exception of forests located at lower elevations which are not well represented. In addition, of the areas of forest cover gained across the study region between 2000 and 2010 (~10,700 km²) only about 15% occurred within panda reserves. Furthermore, accumulated net primary productivity (NPP) per year between 2000 and 2010 across the study region exhibited a monotonic increase, while the relative contribution of the reserve network to this accumulated NPP remained relatively constant (~25.5%). This suggests that the areas inside nature reserves may be reaching their maximum forest cover and NPP levels. Therefore, despite the significant positive roles of these reserves beyond the conservation of the species of interest, further conservation actions are needed to maintain and improve the conservation of regional biodiversity pools, as well as to improve gains in forest cover and in carbon sequestration. The procedures shown in this study are easily transferable to other study regions for assessing the benefits they provide beyond the conservation of the target(s) species of interest.

Key words: carbon sequestration; forest structure; giant panda; net primary productivity; tree species; understory bamboo.

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INTRODUCTION

The degradation of natural ecosystems continues unabated, threatening the long-term survival of many species around the world (Pimm et al. 2014). In response, many conservation efforts have emerged to stop and reverse this degradation, among which the establishment of protected

areas is considered one of the most effective (Hannah et al. 2007, Andam et al. 2008, Jenkins and Joppa 2009). Worldwide there are more than 200,000 protected areas (Juffe-Bignoli et al. 2014), many of which have been established for the conservation of particular species of interest. Yet, their establishment and successful management may entail additional benefits beyond the long-term

survival of the species of interest, including the conservation of entire biodiversity pools and the provision of ecosystem services such as carbon sequestration.

China has seen an impressive rate of nature reserve establishment, particularly over the last decade. By the end of 2014, a total of 2729 nature reserves were established covering ~15% of its land surface (Xu et al. 2017). As one of the world's 17 "mega-diversity" countries (Mittermeier et al. 1997), the establishment of many of these reserves has been driven by the need to protect and restore the habitat of individual endangered and charismatic species such as the tiger (*Panthera tigris amoyensis*), the elephant (*Elephas maximus*), and the giant panda (*Ailuropoda melanoleuca*). Because the latter is considered an icon of biodiversity conservation around the world (Mackinnon and De Wulf 1994, Liu et al. 2001, Loucks et al. 2001), conservation of this species became a national priority. Efforts to conserve the giant panda have been effective, given that its habitat is exhibiting overall gains (Tuanmu et al. 2016), while the species was recently downgraded from "endangered" to "vulnerable" by the International Union for Conservation of Nature (Swaisgood et al. 2016).

Although giant pandas had a wide geographic distribution in the past (Schaller et al. 1985, Reid and Gong 1999), they are currently restricted to six mountain regions in three provinces of China (Reid and Gong 1999, Viña et al. 2010, Liu et al. 2016). The main reason for the reduction in their distribution is human-induced loss and fragmentation of forests, as the pandas rely on forest overstory as shelter and understory bamboo as staple food (Schaller et al. 1985). Therefore, for the specific purpose of protecting and restoring the forests that constitute habitat for the pandas, a network of 67 nature reserves has been designated. These reserves contain about 40% of the entire panda habitat, although they tend to be isolated (Viña et al. 2007, 2010). In addition, in response to major floods in 1998, since the late 1990s the Chinese government has been implementing two of the largest ecological conservation programs in the world: (1) the Natural Forest Conservation Program (NFCP), which bans logging in natural forests, and (2) the Grain-to-Green Program (GTGP), which encourages farmers to return steep cropland to forest by

providing cash, grain, and tree seedlings. While these programs were enacted mainly to increase soil and water retention through the increase in forest cover in mountainous areas, they have global implications as they fulfill part of China's commitment to international biodiversity conservation treaties while also help with climate mitigation through enhanced carbon sequestration (Liu et al. 2008, 2013). Previous studies suggest that these programs have been producing overall positive effects on forests not only at local and regional scales (Viña et al. 2007, 2011, Liu et al. 2008) but also at the national scale (Viña et al. 2016b). The successful implementation of these programs is therefore perceived as promising for the long-term conservation of the giant panda (Tuanmu et al. 2016). In addition, because forests provide many essential ecosystem services to humanity (Foley et al. 2005, Hansen et al. 2013), conservation of the forests that serve as habitat for the pandas also contributes to the provision of numerous ecosystem services. These include soil and water retention, flood mitigation, and carbon sequestration, among others (Ouyang et al. 2016), in addition to providing habitat to numerous other plant and animal species beyond the giant pandas, many of which are also threatened or endangered (Xu et al. 2014, Li and Pimm 2015). Targeting areas for the simultaneous conservation of biodiversity and the provision of ecosystem services make conservation actions, such as the establishment of protected areas, a more efficient endeavor.

To assess the contribution of panda reserves to biodiversity conservation and the provision of ecosystem services, it is crucial to analyze the spatial and temporal dynamics of the structure (e.g., species richness and composition, standing biomass) and function (e.g., net primary productivity [NPP]) of the forests across the giant panda geographic range, both inside and outside reserves. This knowledge provides a reference point for assessing the degree to which panda reserves are enhancing the provision of ecosystem services such as carbon sequestration, as well as protecting biodiversity beyond the target species. While the acquisition of information on forest structure and function across broad geographic regions has been less common than local, stand-based assessments, over the last few years there have been some improvements due to the advent of

advanced remote sensing systems together with novel analytical techniques (Saatchi et al. 2011, Viña et al. 2012, 2016a, Asner et al. 2015).

Using the network of giant panda reserves as a case study, here we evaluate the benefits provided by a network of nature reserves beyond the conservation of a target species. The evaluation was based on the characterization of the structure and function of forests across a broad geographic region both inside and outside the nature reserve network. Characterization of forest structure was conducted by combining data on forest characteristics obtained through field surveys and spaceborne remote sensors. The functional component was characterized by assessing the changes in NPP, a surrogate of carbon sequestration as it measures the amount of atmospheric carbon absorbed through photosynthesis and accumulated as plant biomass (Zhao and Running 2010), between 2000 and 2010 using a remotely derived NPP product.

STUDY AREA

The study area includes six mountain regions (i.e., Qinling, Minshan, Qionglai, Greater Xiangling, Lesser Xiangling, and Liangshan) in three provinces (i.e., Sichuan, Shaanxi, and Gansu) of China where pandas are reported to currently survive (State Forestry Administration 2006, 2015). The region is characterized by high mountains and deep valleys, with elevations between 70 and 6250 m. This strong elevation gradient, combined with complex geology and soils, is responsible for the high biodiversity that characterizes the region, including more than 6000 species of plants in more than 1000 genera, more than 100 species of mammals in 25 families, and around 400 species of birds in 45 families (Reid and Hu 1991, Taylor and Qin 1993a, IUCN 2006). Because of the co-occurrence of many of these species with the pandas, the giant panda is considered an umbrella species, since conservation actions targeting the giant panda may also benefit them (Xu et al. 2014, Li and Pimm 2015).

The extent, structure, and species composition of the natural ecosystems in the study area have been negatively affected by human activities (e.g., logging, agricultural expansion, poaching, medicinal herb collection) for centuries, but particularly during recent decades (Schaller et al.

1985, Reid and Gong 1999, Pan et al. 2001). Therefore, the forests in the region are in various stages of succession, including those inside panda reserves. As giant pandas survive in different types of forest (e.g., broadleaf deciduous, coniferous, mixed) and in different successional stages ranging from young (i.e., 30 yr) secondary forests to old-growth forests (Viña et al. 2007, Bearer et al. 2008), panda reserves comprise not only old-growth forests but also forests in different successional stages. Due to a high biodiversity that is threatened by human activities, the region comprises one of the top 25 biodiversity hotspots in the world (Myers et al. 2000, Mittermeier et al. 2004).

We have been conducting detailed studies on coupled human and natural systems in this region for over two decades (Liu et al. 1999, 2016, An et al. 2002, Linderman et al. 2006, Viña et al. 2007, 2010, Hull et al. 2011, Li et al. 2013). Many results and methods generated from these previous studies in the region have been applied to other regions around the world (Liu et al. 2003, Bawa et al. 2010, An et al. 2014, Bradbury et al. 2014, Carter et al. 2014).

METHODS

Field data

During September–November of 2004, and May–July of 2005–2008, a total of 534 field sampling plots ($\sim 314 \text{ m}^2$) were established in the study region to collect information on land cover and vegetation attributes (e.g., tree stem density, basal area, canopy cover, tree species composition). Among the 534 plots, $\sim 17.8\%$ were located in coniferous forests, $\sim 37.8\%$ in deciduous broadleaf forests, $\sim 15.5\%$ in mixed deciduous–coniferous forests, and $\sim 28.8\%$ in non-forest land cover types (e.g., cropland, grassland, built-up, barren). Field plots under forest cover were located at least 500 m inside the forest to be less affected by edge effects. Topographic (i.e., elevation and slope) and structural (i.e., stem density, basal area, canopy closure, number of tree species, bamboo basal area) characteristics within the plots were recorded. To this effect, the center of each plot was geo-referenced using Global Positioning System receivers. Stem density was established by counting all tree stems within the plot having a diameter at breast height (dbh) equal or higher

than 5 cm. Basal area was determined by measuring the dbh of all the trees counted in the plot. Per-plot canopy closure was determined as the average canopy closure estimated in three to five pictures of the canopy, taken with a digital camera facing upward, while the number of different tree species per plot was also recorded. Finally, as understory bamboo is a conspicuous and dominant characteristic of the forests in the study area, when present, we also recorded bamboo basal area in three $1 \times 1 \text{ m}^2$ subplots randomly distributed within the field plots.

Remotely sensed data

To upscale information from the field plots to the entire study region, we used vegetation phenology as measured by a time series of imagery acquired by the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the National Aeronautics and Space Administration Terra satellite. Moderate Resolution Imaging Spectroradiometer time series imagery were selected not only for their high temporal resolution (i.e., daily acquisition), but also because they cover vast areas, and thus are suitable for analyzing vegetation characteristics across large geographic regions. We used a time series of eight-day composite surface reflectance data acquired between January 2004 and December 2007 (a total of 184 images, 46 for each year) by the MODIS sensor (product MOD09Q1—Collection 5). Time series of the Wide Dynamic Range Vegetation Index (WDRVI) and of the Visible Atmospherically Resistant Vegetation Index (VARI) were calculated from these data using the equations (Gitelson et al. 2002, Gitelson 2004):

$$\text{WDRVI} = \frac{\alpha \cdot \rho_{b2} - \rho_{b1}}{\alpha \cdot \rho_{b2} + \rho_{b1}} \quad (1)$$

$$\text{VARI} = \frac{\rho_{b4} - \rho_{b1}}{\rho_{b4} + \rho_{b1} - \rho_{b3}} \quad (2)$$

where ρ_{b1} , ρ_{b2} , ρ_{b3} , and ρ_{b4} are surface reflectance values in MODIS spectral bands 1 (Red), 2 (Near infrared), 3 (Blue), and 4 (Green), respectively, while α is a coefficient that down-weights the contribution of the near-infrared band, making it comparable to that of the red band (Gitelson 2004). Using a heuristic procedure (Henebry et al. 2004), we selected an $\alpha = 0.25$ as the optimum for the MODIS time series dataset used in

the study. The WDRVI constitutes a non-linear transformation of the widely used Normalized Difference Vegetation Index (NDVI) and is specifically designed to increase the sensitivity to changes in vegetation when the NDVI saturates (Gitelson 2004), making it particularly suitable for assessing forested regions. The VARI is sensitive not only to changes in chlorophyll content (Gitelson et al. 2002, Perry and Roberts 2008), but also to changes of other foliar pigments such as anthocyanins (Viña and Gitelson 2011). Therefore, VARI is useful for detecting changes beyond those solely associated with photosynthetic biomass, such as flowering and fruiting (Viña et al. 2004). Furthermore, the floristic similarity of forest stands in temperate montane forests has been found to be significantly related to the similarity in phenological patterns assessed using VARI (Viña et al. 2012, 2016a). To reduce the effects of temporal autocorrelation in the image time series, principal component analyses were applied to the time series of WDRVI and of VARI. A few principal components (PC) summarize the dominant modes of the spatio-temporal variation, therefore retaining most of the information contained in the image time series (Hall-Beyer 2003).

Numerical analyses

Distribution of different forest types across the study region.—In the field, we sorted the different forest types into coniferous, broadleaf deciduous, and mixed coniferous–broadleaf deciduous forest stands. The coniferous and mixed coniferous–broadleaf deciduous forests were further sorted into “planted” and “natural” stands. This sorting was not applied to the broadleaf deciduous forest stands because most of them were the product of natural regeneration.

The PC imagery derived from the MODIS-WDRVI image time series, together with the locations of the field sampling plots under coniferous, broadleaf deciduous, and mixed coniferous–broadleaf deciduous forest types, was used in a fuzzy classification algorithm, to map the distribution of each of these different forest types across the study region. Because a low accuracy was obtained in the separation between planted and natural stands, a classification of the PC obtained from the WDRVI image time series was performed only to separate among coniferous,

broadleaf deciduous, and mixed coniferous–broadleaf deciduous forest types. The fuzzy classification algorithm used was based on the principle of maximum entropy (Jaynes 1957) and applied using the software MaxENT (Phillips et al. 2006). Output maps represent a probability of each pixel to be coniferous, broadleaf deciduous, and mixed coniferous–broadleaf deciduous forest types. These output probability maps were validated using a cross-validation procedure in which two-thirds of the ground truth field plots were used for calibration while the remaining one-third were used for validation. To reduce dependence on a single random partition into calibration and validation, we generated 10 different random partitions to be used in 10 different fuzzy classifications, which were then averaged. The 10 output probability maps were validated by means of a receiver operating characteristic (ROC) curve (Hanley and Mcneil 1982). The ROC curve is a plot of the sensitivity values (i.e., true positive fraction) vs. their equivalent 1-specificity values (i.e., false positive fraction) for all possible probability thresholds. The area under the ROC curve (AUC) is a measure of model accuracy, with AUC values ranging from 0 to 1. The three output probability maps (i.e., probability of coniferous, broadleaf deciduous, and mixed coniferous–broadleaf deciduous forest types) exhibited average AUC scores of 0.965, 0.969, and 0.926, respectively, denoting a high accuracy.

Using the ISODATA unsupervised classification algorithm (Jensen 2005), the three output probability maps (i.e., probability of coniferous, broadleaf deciduous, and mixed coniferous–broadleaf deciduous forest types) were merged into a single choropleth map. We used a maximum of 1000 iterations with a convergence (the maximum percentage of the pixels whose class values are allowed to be unchanged between iterations) specified at 0.95, producing an output of four internally homogenous land cover types (i.e., coniferous forest, broadleaf deciduous forest, mixed coniferous–broadleaf deciduous forest, and non-forest). While this procedure collapsed the spatial variability present in the probability maps, it allows quantification of the areas under the four different land cover types.

Plant species diversity across the study region.—Previous work within the study region has shown that at local and regional scales, floristic

similarity is significantly related to the phenologic similarity evaluated using time series of the VARI index (Viña et al. 2012, 2016a). Therefore, the VARI-based phenologic similarity can be used as a surrogate for assessing species turnover across broad geographic regions. Based on this premise, we applied the ISODATA unsupervised classification algorithm (Jensen 2005) to the PC derived from the VARI image time series, to obtain a choropleth map of internally homogeneous clusters, each denoting a floristically similar forest class. The ISODATA algorithm used a maximum of 1000 iterations with a convergence specified at 0.95. To assess the optimal number of clusters, we used an iterative process that increased the number of output clusters and calculated the Euclidean distance among all clusters in each iteration. We then plotted the average inter-cluster Euclidean distance against the number of clusters and chose the inflection point as the one denoting the optimal number of clusters.

Temporal dynamics of forest cover and net primary productivity.—The temporal dynamics of forest cover in the study region were based on a previous analysis of forest cover across all of China (Viña et al. 2016b), using the MODIS-derived Vegetation Continuous Fields (VCF) Tree Cover product (Hansen et al. 2003). Using the MODIS-VCF, we evaluated changes in forest cover in the study region from 2000 to 2010 using a change detection analysis and a trend analysis. Details on these procedures are given in Viña et al. (2016b).

To assess the changes in NPP during the same period (i.e., 2000–2010), we used the Terra/MODIS NPP MOD17A3 product. This dataset was re-sampled and co-registered to the MODIS-VCF product (i.e., 250 m/pixel). Total NPP values per year were integrated across the entire study region to obtain a regional annual NPP estimate, and the relative contribution of the panda reserves to the total NPP per year was calculated. Finally, all pixels within the study region were evaluated to determine whether they exhibited significant ($P < 0.01$) trends in decadal (2000–2010) NPP values. Pixels with no significant NPP trends were assumed not to have changed in NPP between 2000 and 2010. The relative change (percent change in NPP between 2000 and 2010) was then calculated for the pixels exhibiting a significant trend in NPP.

RESULTS

Structural characteristics

Across the current giant panda geographic range, forests occupy $\sim 32,890 \text{ km}^2$, corresponding to $\sim 27\%$ of the entire study area (i.e., six mountain regions in three provinces; Fig. 1). Coniferous, broadleaf deciduous, and mixed coniferous–broadleaf deciduous forest types comprise $\sim 47.6\%$, 30.4% , and 22.0% of the total area of forests, respectively (Figs. 1, 2). Among the areas classified as panda habitat in the study region (Viña et al. 2010), coniferous, broadleaf deciduous, and mixed coniferous–broadleaf deciduous forest types comprise $\sim 44.5\%$, 28.3% , and 27.2% , respectively (Fig. 2). In addition, among giant panda nature reserves (which occupy $\sim 27.7\%$ of the study region), coniferous, broadleaf deciduous, and mixed coniferous–broadleaf deciduous

forest types comprise $\sim 49.3\%$, 25.4% , and 25.3% of the forest cover, respectively (Fig. 2).

Natural coniferous and mixed forest stands exhibit, on average, higher canopy heights than those under the other forest types (Fig. 3A), while planted coniferous forest stands exhibit, on average, the highest stem densities (Fig. 3B). With respect to canopy closure, broadleaf deciduous forest stands exhibit, on average, the highest values (Fig. 3C), followed by mixed stands (both planted and natural). Coniferous forests (both planted and natural) exhibit, on average, the lowest canopy closures (Fig. 3C). Additionally, natural coniferous forest stands exhibit the highest basal areas, followed by planted coniferous forests, while deciduous and mixed forest stands on average exhibit comparatively lower basal areas (Fig. 3D).

Dominant tree species sampled across the panda range were *Betula albo-sinensis*, *Acer*

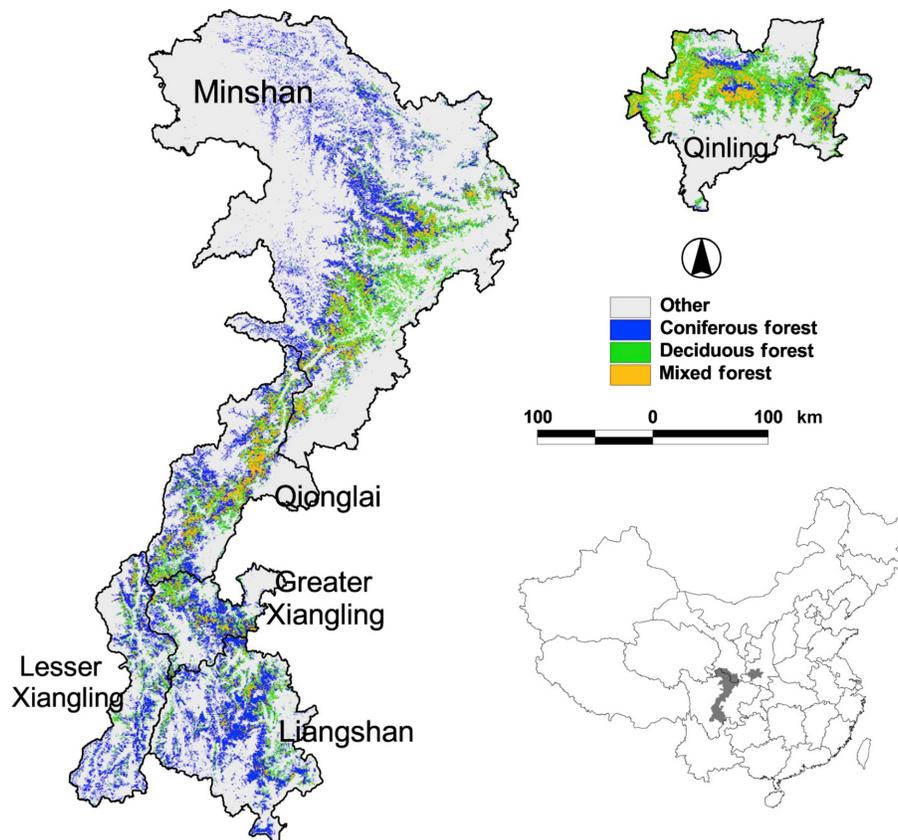


Fig. 1. Moderate Resolution Imaging Spectroradiometer-derived distribution of coniferous, broadleaf deciduous, and mixed coniferous–broadleaf deciduous forests in the mountain regions comprising the geographic range of the giant panda.

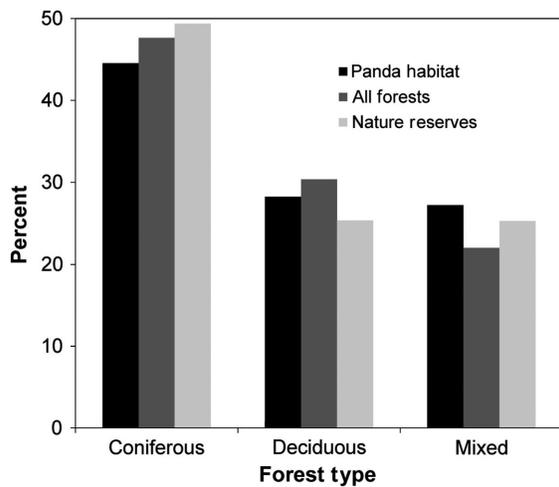


Fig. 2. Proportion of coniferous, broadleaf deciduous, and mixed coniferous–broadleaf deciduous forests across all forests in the study region (Fig. 1), across panda habitat areas, and across forests within nature reserves.

oliverianum, *Betula utilis*, *Cyclobalanopsis glauca*, *Pinus armandii*, *Toxicodendron vernicifluum*, and *Litsea pungens*. Broadleaf deciduous and mixed (both planted and natural) forests on average exhibited the highest tree species richness per plot, while coniferous forests (both planted and natural) exhibited the lowest values (Fig. 4). In addition, bamboo was a conspicuous understory characteristic of the forests across the study area, as it was present in ~69% of all the forest field plots sampled. A total of 23 bamboo species were sampled across the entire study area, among which *Fargesia qinlingensis*, *Bashania fargesii*, *Bashania fangiiana*, *Fargesia dracocephala*, and *Fargesia denudata* were the most common. However, the occurrence of understory bamboo species was more common in field plots located in broadleaf deciduous forest stands (present in ~79%) and mixed forest stands (present in ~78%) than in field plots located in coniferous stands

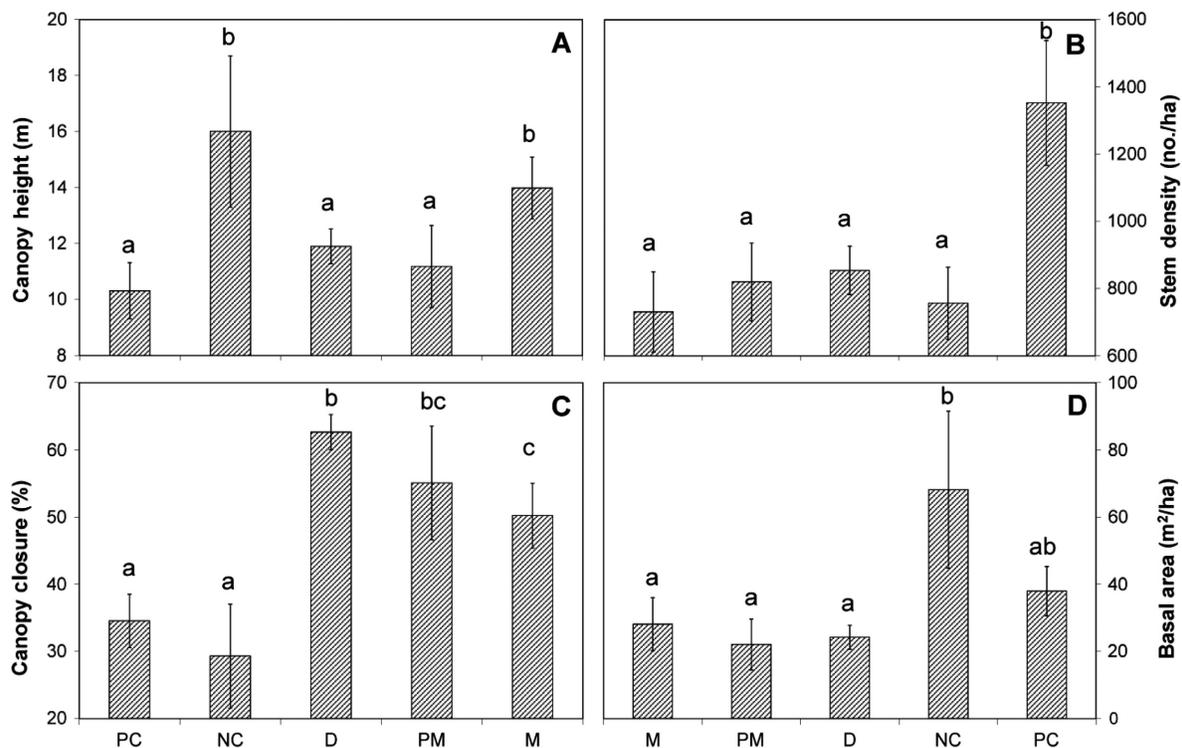


Fig. 3. Structural characteristics of different forest types: PC, planted coniferous forest; NC, natural coniferous forest; D, broadleaf deciduous forest; PM, planted mixed coniferous–broadleaf deciduous forest; M, natural mixed coniferous–broadleaf deciduous forest. (A) Average canopy height. (B) Average stem density. (C) Average canopy closure. (D) Average basal area. Error bars correspond to 2 SEM. Columns with a different letter are significantly different as determined by Bonferroni-corrected post hoc Mann–Whitney *U*-tests.

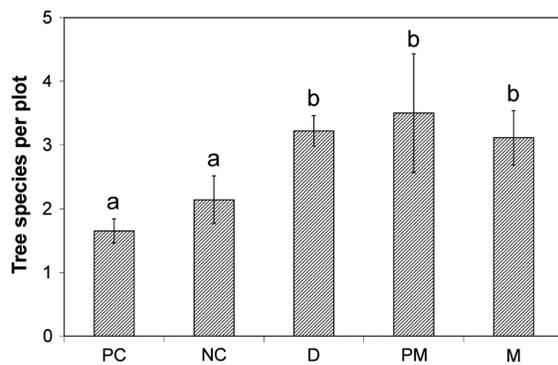


Fig. 4. Average tree species per field plot among different forest types: PC, planted coniferous forest; NC, natural coniferous forest; D, broadleaf deciduous forest; PM, planted mixed coniferous–broadleaf deciduous forest; M, natural mixed coniferous–broadleaf deciduous forest. Error bars correspond to 2 SEM. Columns with a different letter are significantly different as determined by Bonferroni-corrected post hoc Mann–Whitney *U* tests.

(present in ~40%). Furthermore, among the field plots located in planted coniferous stands, understory bamboo species occurred only in ~34%. With the exception of field plots located in planted coniferous forest stands, all forest field plots that had understory bamboo exhibited, on

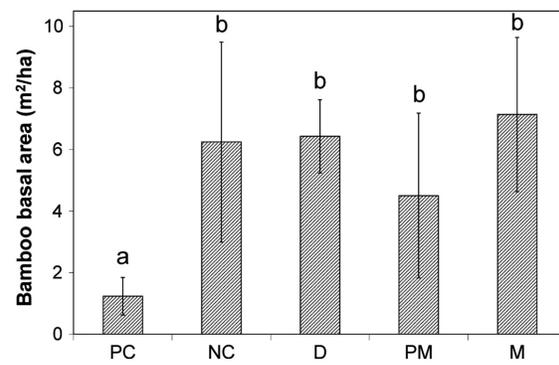


Fig. 5. Average bamboo basal area among different forest types: PC, planted coniferous forest; NC, natural coniferous forest; D, broadleaf deciduous forest; PM, planted mixed coniferous–broadleaf deciduous forest; M, natural mixed coniferous–broadleaf deciduous forest. Error bars correspond to 2 SEM. Columns with a different letter are significantly different as determined by Bonferroni-corrected post hoc Mann–Whitney *U* tests.

average, a comparable bamboo biomass (represented as bamboo basal area in Fig. 5).

The first three PC obtained from the MODIS-VARI image time series (explaining 82% of the total variance in the image time series) were used to develop a choropleth map of 20 clusters using

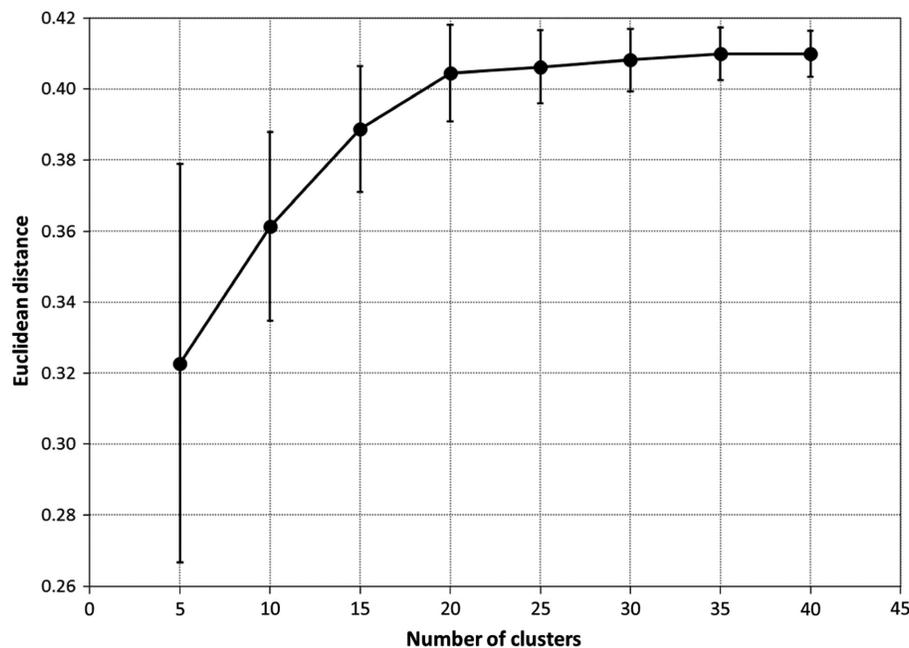


Fig. 6. Inter-cluster Euclidean distance vs. number of clusters. The inflection point (at around 20 clusters) represents the optimal number of clusters to be obtained. Error bars represent 1 SEM.

the ISODATA algorithm. Twenty was deemed the optimal number of clusters given that inter-cluster Euclidean distance reached an inflexion point at around 20 clusters (Fig. 6). Each of these clusters represents an internally homogenous floristic class, while among them they tend to be floristically dissimilar. The output 20-cluster choropleth

map (Fig. 7) was used to evaluate nature reserve representativeness of tree biodiversity. Results show that 18 out of the 20 floristic clusters have more than 20% of their area inside nature reserves, while clusters 19 and 20 have < 20% (Fig. 7). These two clusters tend to be located at lower elevations (<2000 m; Fig. 8) and are dominated by broadleaf

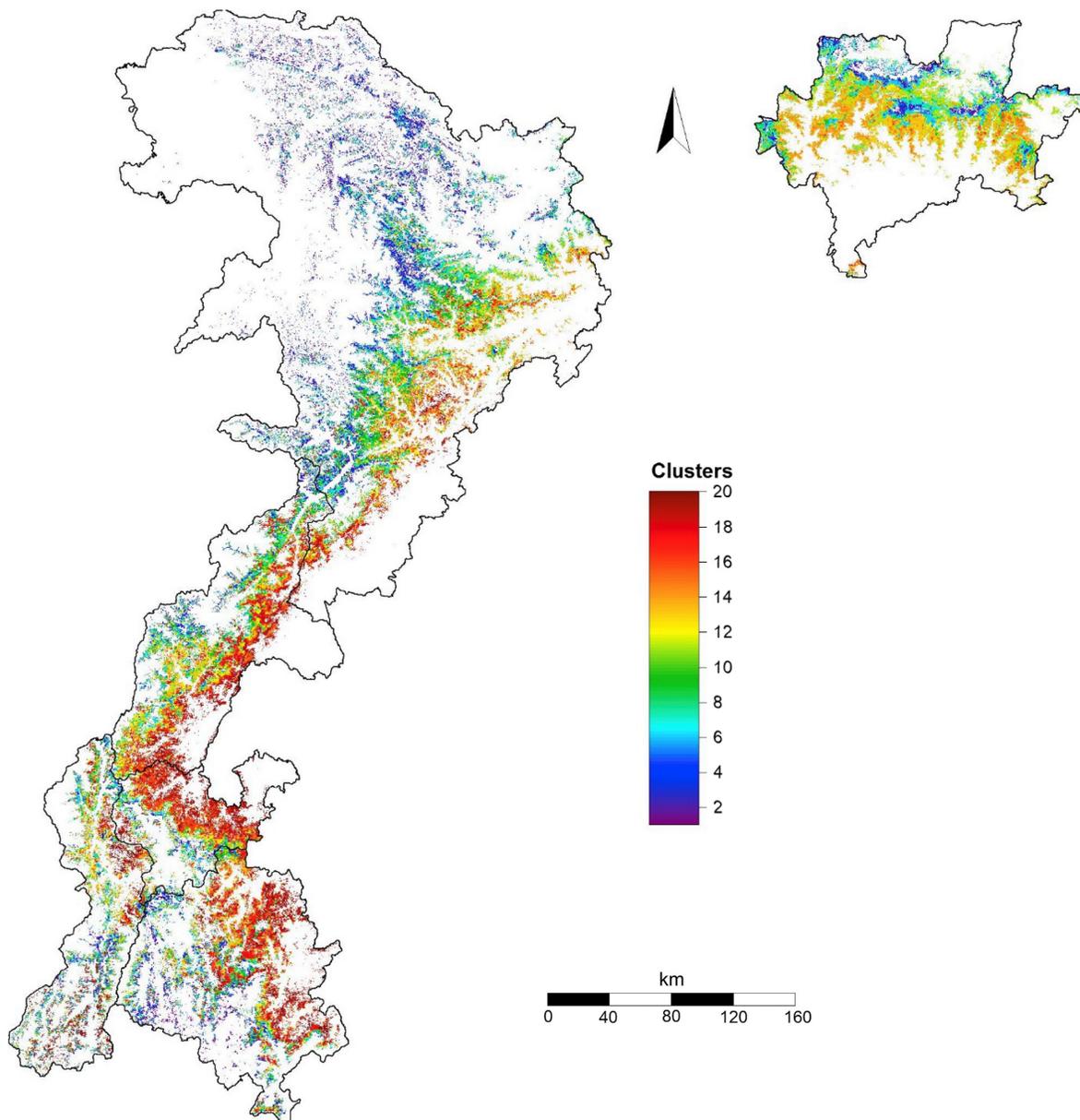


Fig. 7. Map of floristically similar areas (clusters) within the study region. This map was obtained by applying a non-hierarchical cluster analysis (ISODATA) to three principal components obtained from a Moderate Resolution Imaging Spectroradiometer-derived VARI image time series (2004–2007).

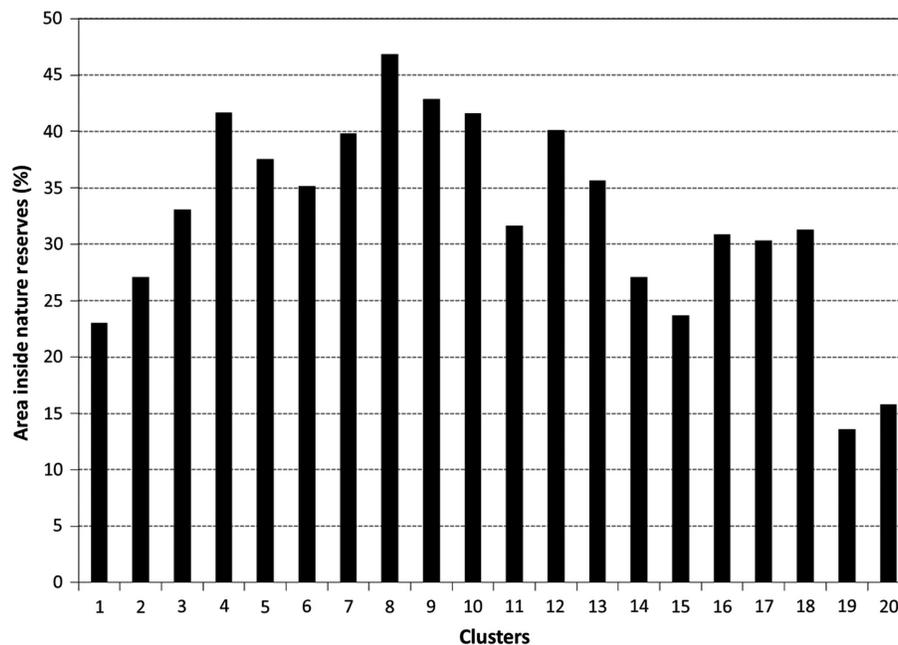


Fig. 8. Relative area of each floristic cluster (depicted in Fig. 7) located within panda nature reserves.

tree species such as *B. utilis*, *Castanopsis sclerophylla*, *L. pungens*, and *Salix cupularis*.

Functional characteristics

Between 2000 and 2010, the study region exhibited a monotonic increase in the total accumulated NPP per year (Fig. 9A), while the proportion of total accumulated NPP per year inside nature reserves remained relatively constant (varying around 25.5%; Fig. 9B). Over the same time period, the entire study area gained around 10,700 km² of forest cover through a combination of natural regeneration and tree plantation, while it lost around 740 km² (Fig. 10A). Of the forest cover gained and lost, about 15% and 36% occurred within panda reserves, respectively. In addition, the study region exhibited a per-pixel average increase in NPP of about 10.9% (Fig. 10B). While significant changes in NPP occurred in some areas that observed gains in forest cover, not all areas that exhibited a gain in forest cover experienced a significant change in NPP and vice versa (Fig. 10).

DISCUSSION

Results of this study show some of the hidden roles that a network of protected areas

established for the conservation of a species of interest have on the conservation of biodiversity and on the provision of ecosystem services. In our study region, forests occupy about one-third of its total area and are dominated by coniferous stands. The coniferous forests of the study area tend to have higher accumulated woody biomass than the broadleaf deciduous and mixed coniferous–broadleaf deciduous forests, given their larger average basal areas, larger average stem densities (particularly the planted assemblages), and higher average canopy heights. Notwithstanding their higher woody biomass, coniferous forests tend to exhibit significantly lower canopy closures, which allow solar radiation to reach more easily the understory. Nevertheless, despite this lower canopy closure, bamboo biomass is not significantly higher, and in fact, it is significantly lower in planted coniferous forests than in all other forest types. This suggests that the development of understory bamboo, which constitutes a crucial component of the giant panda habitat (Schaller et al. 1985, Johnson et al. 1988, Liu et al. 1999, Viña et al. 2007, Bearer et al. 2008) and is driven by a complex combination of canopy structural characteristics (Taylor and Qin 1989, 1993b, Taylor et al. 2004, Liu and Viña 2014), may be inhibited in planted coniferous

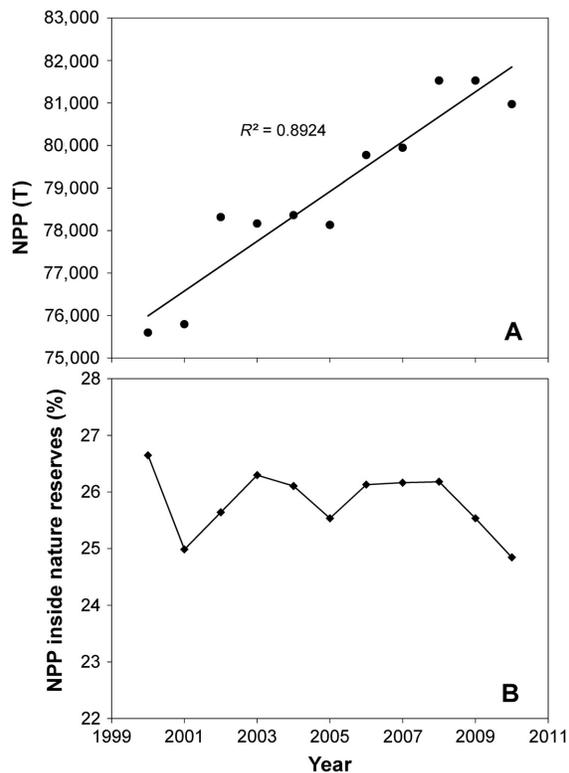


Fig. 9. (A) Total net primary productivity (NPP) per year accumulated across the entire giant panda geographic range. (B) Proportion (in percent) of the total NPP per year within panda nature reserves.

forests. Thus, to restore suitable habitat for the giant pandas it is necessary to go beyond planting monospecific coniferous, and usually exotic, tree stands, but to establish suitable structural characteristics that enhance the development of understory bamboo. When secondary forests contain understory bamboo, they become suitable habitat for the pandas, even if they are young stands (i.e., ~30 yr; Viña et al. 2007, Bearer et al. 2008).

Tree species richness in the study area tends to be comparatively low in coniferous forests as compared to broadleaf deciduous and mixed coniferous–broadleaf deciduous forests, particularly in planted assemblages. If planted assemblages are not occupied by broadleaf tree species (thus making them planted mixed coniferous–broadleaf deciduous stands), their average tree species richness is between 1 and 2. However, to allow the occurrence of tree species different from the planted ones it is necessary to combine tree

planting with natural regeneration through a reduction in the stem density of planted trees. While this may reduce the amount of standing biomass over a short temporal window, over the long run it will allow plantation forests to exhibit structural traits similar to those of mixed broadleaf deciduous–coniferous stands, with comparable tree species richness.

Our model for evaluating tree species diversity across the study region, based on the close relationship between floristic and phenologic similarity, allowed us to evaluate the regional tree species diversity represented inside nature reserves as compared to the regional biodiversity pool. Such assessment is also suitable for driving further field studies, and for targeting areas that may require additional conservation efforts. In our case, the current panda nature reserve network is representative of the plant biodiversity pool present across the current panda geographic range. As such, the nature reserves established for the giant panda are also contributing to the conservation of numerous species present across the panda geographic range. In addition, the procedure also allowed us to identify conservation gaps (clusters 19 and 20 in Fig. 8) where the panda reserves should expand, either through an increase in the extension of current reserves or through the addition of new ones. Nevertheless, as it requires high-temporal resolution remotely sensed data, which are normally acquired at coarse spatial resolutions (e.g., 250 × 250 m/pixel or larger), a limitation of this procedure is that it may not completely relate to the spatial resolution at which the field data are normally acquired (e.g., 30 × 30 m field plots). Yet, it is possible to reduce this limitation through the fusion of remotely derived datasets with different temporal and spatial resolutions (Viña et al. 2016a).

The study region experienced a conspicuous and significant increase in forest cover between 2000 and 2010. This increase has been attributed to the natural regeneration and tree plantation that occur through the successful implementation of conservation policies, including the establishment of panda reserves and of the NFCP and the GTGP (Viña et al. 2007, 2011, Li et al. 2013, Liu et al. 2016, Tuanmu et al. 2016). However, because many forests lack suitable understory bamboo, only about 17% of the forested areas constitute suitable habitat for the pandas. Coniferous forests account for the highest amount of

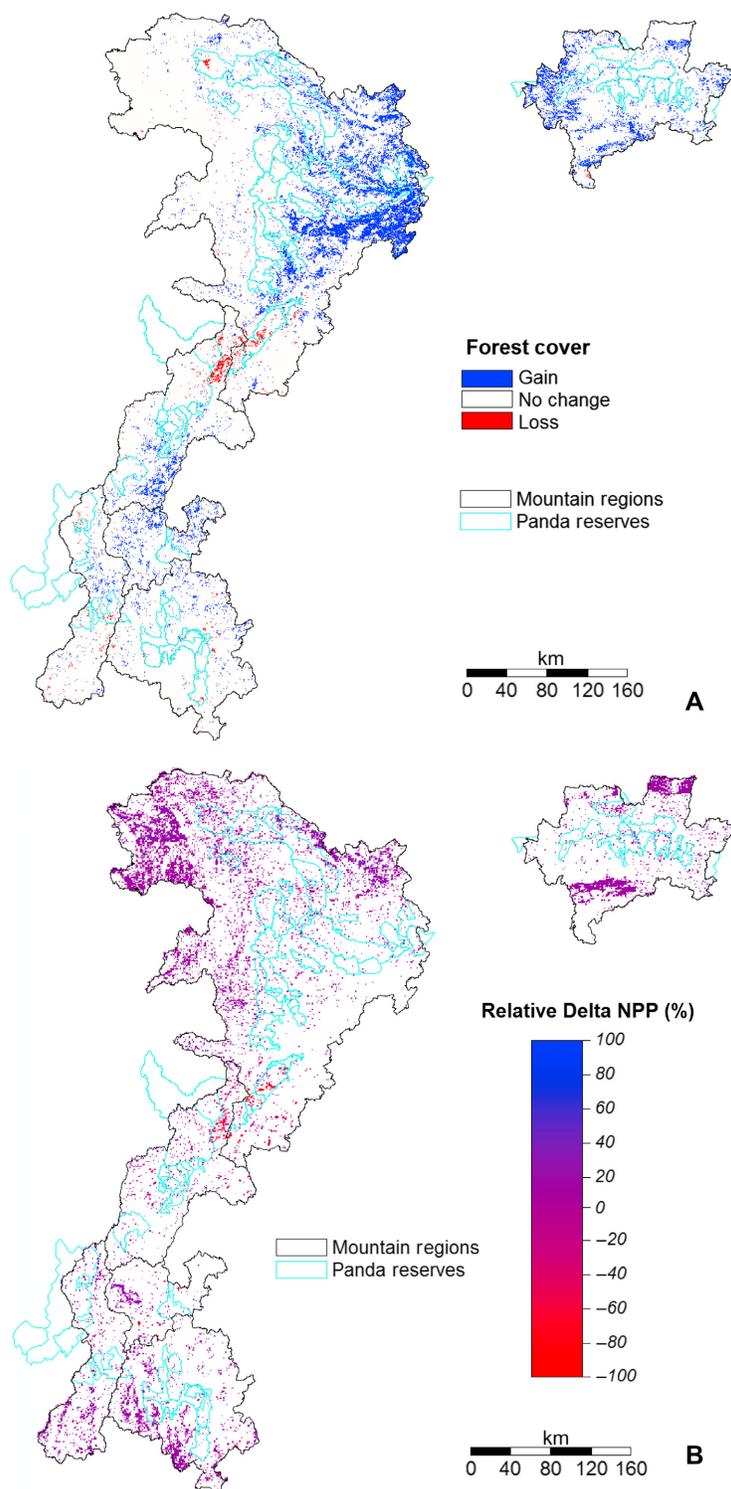


Fig. 10. (A) Map of areas that experienced gains and losses of forest cover in the study region between 2000 and 2010. (B) Map of per-pixel relative change (delta) in net primary productivity in the study region between 2000 and 2010.

panda habitat (~44.5%), most of which is composed of natural stands at higher elevations, given that planted coniferous forest stands tend to lack understory bamboo. Broadleaf deciduous and mixed coniferous–broadleaf deciduous forest stands each account for less than one-third of the panda habitat, many of which are stands under natural regeneration. Thus, forests under natural regeneration tend to have more understory bamboo suitable for the giant pandas than their planted counterparts. This needs to be considered for a successful inclusion of giant panda habitat conservation/restoration activities into national forest conservation programs such as the NFCP and the GTGP. We suggest that the managers of these programs consider natural forest regeneration over tree planting in their operations, and discourage the practice of planting exotic tree species (e.g., the Japanese Larch, *Larix* spp.) which prevent the development of understory bamboo species suitable for the giant panda.

Although related to the gain in forest cover only in few areas, the study region experienced a significant increase in NPP within the same time frame. This increase suggests that not just forest cover but the biomass of other types of vegetation in the study region is increasing, and therefore, they are having positive effects on carbon sequestration. However, less than one-fifth of the areas of forest gain observed in the study region occurred inside panda reserves, while panda reserves maintained a relatively constant proportion of the total accumulated NPP per year (~25.5%). This suggests that the vegetation and the forest cover within these reserves seem to be closer to their maximum biomass levels than outside them. Therefore, to obtain additional gains in forest cover and carbon sequestration, future conservation actions should particularly target areas outside panda reserves, but without reducing current conservation activities within current panda reserves. However, one limitation of this analysis is that it only focused on NPP dynamics as a surrogate of carbon sequestration while neglecting many other functional traits of forests that also constitute crucial ecosystem services, such as soil and water retention and flood prevention (Ouyang et al. 2016). Nevertheless, while our selection of NPP as a functional trait was solely driven by its public availability in lattice format, it does not preclude using other variables

readily available for assessing different ecosystem services (Yang et al. 2013, Xu et al. 2017).

CONCLUSIONS

Protected areas perform multiple roles that go beyond their intended conservation purposes, many of which go unnoticed and thus are seldom targeted for improvement. Such is the case of giant panda reserves which are generating benefits beyond giant panda conservation, since they are significantly contributing to the conservation of entire plant biodiversity pools and to the provision of ecosystem services such as carbon sequestration. However, the floristic composition of forests located at lower elevations is less represented within the panda reserve system, while the observed gains in both forest cover and NPP (thus carbon sequestration) did not particularly occur within panda reserves, perhaps because they are reaching their maximum forest cover and NPP levels. Thus, it is necessary to expand the areas under conservation (e.g., development of new reserves and extensions to the areas of current reserves), especially in regions exhibiting higher gains in forest cover and carbon sequestration, as well as those located at lower elevations whose biodiversity is less represented in the current panda reserves, even though panda occurrence in these areas is less common. Such areas may become even more important under the context of the projected negative effects of climate change on species distribution (Tuanmu et al. 2013) and on carbon sequestration (Melillo et al. 2016).

The procedures shown in this study are based on remotely sensed data acquired by operational satellite sensor systems collecting data across the globe and that are publically and freely available. Therefore, they are easily transferable to other study regions for assessing the benefits of nature reserves beyond the conservation of a target species of interest. Such assessments will allow identifying areas that require further conservation actions, as well as those that are contributing to biodiversity conservation and ecosystem services provision beyond their intended conservation targets. As such, our results directly respond to recent calls for an efficient prioritization of the location of protected areas (Joppa and Pfaff 2009).

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