

*Assessing the effects of payments for
ecosystem services programs on forest
structure and species biodiversity*

**Hsiang Ling Chen, Rebecca L. Lewison,
Li An, Yu Hsin Tsai, Douglas Stow, Lei
Shi & Shuang Yang**

Biodiversity and Conservation

ISSN 0960-3115

Volume 29

Number 7

Biodivers Conserv (2020) 29:2123-2140

DOI 10.1007/s10531-020-01953-3

Your article is published under the Creative Commons Attribution license which allows users to read, copy, distribute and make derivative works, as long as the author of the original work is cited. You may self-archive this article on your own website, an institutional repository or funder's repository and make it publicly available immediately.



Assessing the effects of payments for ecosystem services programs on forest structure and species biodiversity

Hsiang Ling Chen, et al. [full author details at the end of the article]

Received: 18 June 2019 / Revised: 4 February 2020 / Accepted: 22 February 2020 /
Published online: 27 February 2020
© The Author(s) 2020

Abstract

Globally, biodiversity has declined at an unprecedented rate, challenging the viability of ecosystems, species, and ecological functions and their corresponding services. Payments for ecosystem services (PES) programs have been established and implemented worldwide to combat the degradation or loss of essential ecosystems and ecosystem services without sacrificing the well-being of people. With an overarching goal of reducing soil erosion, China's Grain-to-Green program (GTGP) converts cropland to forest or grassland. As one of the largest PES programs in the world, GTGP has great potential to offer biodiversity conservation co-benefits. To consider how GTGP may influence biodiversity, we measured forest structure and plant and wildlife species diversity at both GTGP forest and natural forest sites in Fangjingshan National Nature Reserve, China. We also evaluated the relationship between canopy cover and biodiversity measures to test whether forest cover, the most commonly measured and reported ecological metric of PES programs, might act as a good proxy for other biodiversity related parameters. We found that forest cover and species diversity increased after GTGP implementation as understory and overstory plant cover, and understory and midstory plant diversity at GTGP sites were similar to natural forest. Our results suggest that GTGP may also have been associated with increased habitat for protected and vulnerable wildlife species including Elliot's pheasant (*Syrnaticus elliotti*), hog badger (*Arctonyx collaris*), and wild boar (*Sus scrofa*). Nevertheless, we identified key differences between GTGP forest and natural forest, particularly variation in forest types and heterogeneity of overstory vegetation. As a result, plant overstory diversity and wildlife species richness at GTGP forest were significantly lower than at natural forest. Our findings suggest, while forest cover may be a good proxy for some metrics of forest structure, it does not serve as a robust proxy for many biodiversity parameters. These findings highlight the need for and importance of robust and representative indicators or proxy variables for measuring ecological effects of PES programs on compositional and structural diversity. We demonstrate that PES may lead to biodiversity co-benefits, but changes in

This article belongs to the Topical Collection: Forest and plantation biodiversity.

Communicated by David Hawksworth.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10531-020-01953-3>) contains supplementary material, which is available to authorized users.

program implementation could improve the return on investment of PES programs to support conservation of biodiversity.

Keywords Grain-to-Green program · Fanjingshan National Nature Reserve · Hierarchical occupancy models · Species richness · Forest cover · China

Introduction

Ecosystem services, defined as benefits (direct or indirect) that wild organisms or ecosystems provide to people, have been identified as necessary for human survival and well-being¹ (Millennium Ecosystem Assessment 2005; Harrison et al. 2010). Ecosystem services are typically categorized as provisioning, regulating, supporting, or sociocultural services (Ferraro and Kiss 2002; Wunder 2007). Although there is considerable complexity in the link between biodiversity and ecosystem services (Balvanera et al. 2014), biodiversity has been recognized as an essential component that maintains vital ecological processes and corresponding services (Díaz and Cabido 2001; Hoekstra et al. 2005; Cardinale et al. 2012). Biodiversity can regulate ecological processes, support production of other services such as soil productivity and crop pollination, and generate services with cultural values (e.g. presence of large carnivores) (Mace et al. 2012; Quijas et al. 2019). Globally, there has been substantial decline in biodiversity which has led to degraded ecosystems and their corresponding ecosystem services (Cardinale et al. 2012; Newbold et al. 2016; IPBES 2019). To address threats of human activity on ecosystems while recognizing the socio-economic needs of human communities, a management approach called payments for ecosystem services (PES) has been established and implemented in many countries. PES programs aim to protect ecosystem services while supporting sustainable livelihoods or alleviating poverty by providing financial or in-kind incentives directly to resource users to undertake environmentally desirable actions or avoid environmental damaging ones (Wunder 2007, 2013; Jack et al. 2008; Mathieu et al. 2018). While PES programs mostly are designed to improve regulating services (e.g. water quality, erosion control), additional services such as biodiversity are commonly cited as a secondary benefit (Prager et al. 2016; Bremer et al. 2019). For example, the Natural Forest Conservation Program (NFCP) in China was enacted primarily for flood control, however, the program has also improved habitat for wildlife by restoring natural forest (Liu et al. 2008).

Despite widespread implementation of PES programs and numerous calls for improved assessments of the ecological effectiveness of PES programs, most PES evaluations do little to directly measure ecological metrics on the ground (Yin et al. 2013; Naeem et al. 2015; Daw et al. 2016; Lewison et al. 2017). Instead, PES evaluations

¹ In this paper, we take an ecological perspective of biodiversity, believing that “diversity” per se in ecosystems is important to ecosystem function and ecological services” (Miller et al. 2014). We acknowledge the existence of other conservation ethics or ideologies such as the one proposed by Kareiva et al. (2007), Kareiva and Marvier (2012), which challenges the traditional goal and practice of conservation for not paying enough attention to ecosystem resilience (e.g., some species can survive human disturbances or get recovered quickly), the role of managed ecosystems or people-friendly ecosystems (e.g., these systems can also maintain high levels of species diversity), and social justice (e.g., displacing indigenous people when setting up nature reserves). Although a detailed presentation of conservation ethics is beyond the scope of this paper, we acknowledge the importance of this perspective and refer readers with interest to relevant literature (e.g., Miller et al. 2014; Kareiva et al. 2007; Kareiva and Marvier 2012).

typically report program success based on measures of program compliance and land cover and land use change, which is assumed to be a good proxy for other ecological elements such as species composition, species richness, and ecosystem function (Brouwer et al. 2011; Miteva et al. 2012; Yin et al. 2013). For example, in a review of primary literature on nine PES programs in Costa Rica and Mexico (see Table 3 in Miteva et al. 2012), the authors found that land cover and land use change are the only ecological parameter or outcome monitored for the PES programs. A more recent review of 118 PES programs worldwide demonstrated that even in PES programs that identified supporting biodiversity as a primary goal, more than 65% of the programs had not published biodiversity data to date (Prager et al. 2016). Although there are a few PES program evaluations that have measure the associated effects of PES on ecosystem outputs and biodiversity (Hua et al. 2016; Basham et al. 2016; Wu et al. 2017), the impact of PES programs on plant or animal structure or species biodiversity remains understudied.

The lack of direct evidence on how PES programs affect biodiversity is not surprising given the general challenges associated with policy evaluation (Miteva et al. 2012; Yin et al. 2013), which require long-term monitoring, data collection, and ideally a BACI (Before-After, Control-Impact) or counterfactual study design (Baylis et al. 2016). Despite these challenges, investigating current structural and species diversity at PES sites relative to more intact landscape can provide insights of the ecological effectiveness of PES beyond the commonly used metric- land cover and land use change (Lewison et al. 2017). Moreover, identifying differences between PES sites and natural sites provides information that can improve PES implementation and support management and conservation of biodiversity and related ecosystem services.

The Grain-to-Green Program (GTGP), also known as the Sloping Land Conversion Program in China, is one of the largest PES programs in the world (Liu et al. 2008). Despite China's high level of species biodiversity, rapid human population growth and land transformation have degraded ecosystems and threatened persistence of hundreds of species (World Bank 2001; Liu 2003). To address mounting environmental crises and improve ecosystem services, large-scale programs of terrestrial ecosystem restoration like GTGP have been implemented (Yin and Yin 2010). GTGP, like many PES programs around the world, was implemented to reduce soil erosion and runoff with biodiversity restoration as a secondary consideration (Xu et al. 2006; Hua et al. 2016). GTGP converts cropland on steep slopes to forest and grassland while compensates participating farmers with cash and grain (Liu et al. 2008). Since 2013, over 27 million hectares of GTGP forest have been established (Hua et al. 2016), and water surface runoff and soil erosion have declined (Liu et al. 2008).

With accelerating biodiversity loss (Newbold et al. 2016), and the unparalleled scale of China's PES land management policy (Hua et al. 2016), GTGP provides an opportunity to provide co-benefits to biodiversity and related ecosystem services (Wang et al. 2007), such as wildlife habitat, recreation and ecotourism (Quijas et al. 2019). In this study, we use Fanjingshan National Nature Reserve (FNNR) in China as a case study site to examine effects of GTGP on forest structure and plant and wildlife species diversity. By measuring plant community composition, structure, and wildlife occupancy at both GTGP and natural forest sites, we ask whether PES programs not directly designed for biodiversity conservation, can generate biodiversity and conservation co-benefits. We also consider how changes in forest canopy cover, the most commonly measured and used in PES evaluations, are related to other metrics of structural and species biodiversity. Our exploration of the relationship between PES and forest canopy cover, forest structure, and species biodiversity measures highlights how large-scale PES land

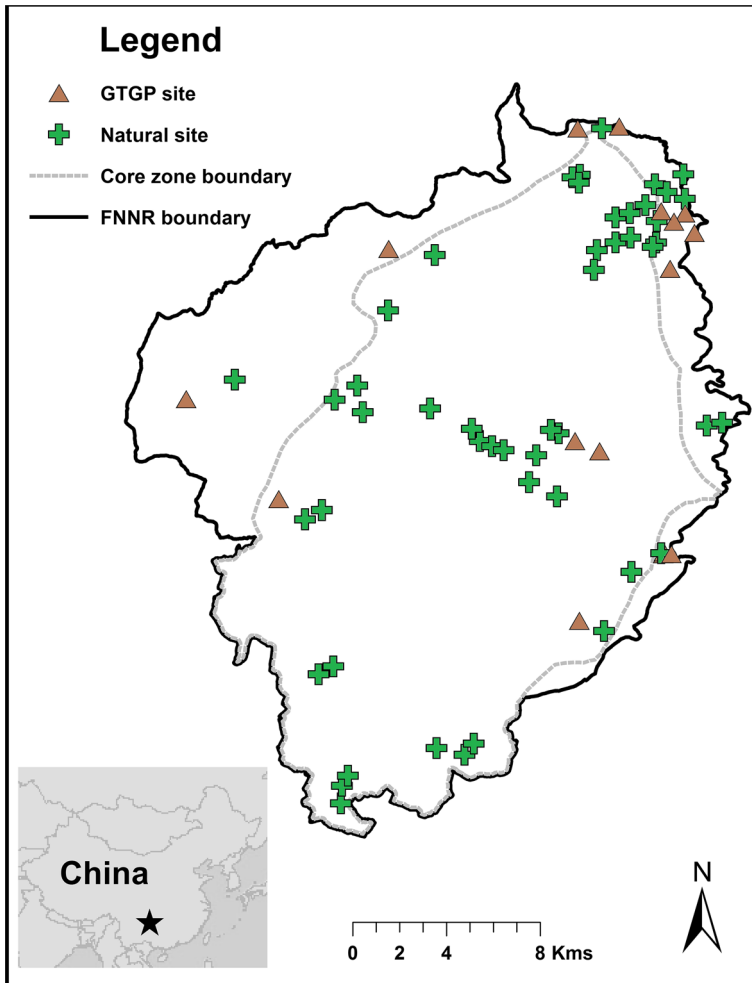


Fig. 1 Sampling plots for vegetation and wildlife survey in forest established by Grain-to Green Programs ($n=16$) and in natural forest ($n=49$) in Fanjingshan National Nature Reserve, China, 2015–2016

management programs, like GTGP, can influence biodiversity and, if so, how those benefits can be measured.

Methods

Study area

Fanjingshan National Nature Reserve ($27^{\circ} 55' 11.2''$ N $108^{\circ} 41' 50.1''$ E, Fig. 1) in Guizhou Province, China was established in 1978 as a protected area for the endangered Grey snub-nosed monkey (*Rhinopithecus brelichi*), and then extended to the conservation of other animal and plant species protected under the Law of the People's Republic of China on the

Protection of Wildlife, such as the Asiatic black bear (*Ursus thibetanus*), Elliot's pheasant (*Syrnaticus ellioti*), and the dove-tree (*Davidia involucrata*) (Wu et al. 2004). The reserve, spanning 419 km² with nearly 2000 m of vertical relief, has over 95% of forest cover, ranging from evergreen broadleaf forest at low elevations (around 700 m), to mixed deciduous-broadleaf ecosystems at mid-elevations (1000–1300 m), up to subalpine, meadow, and conifer ecosystems at higher elevations (1600–2600 m) (Yang et al. 2002). The reserve contains a large amount of undisturbed primary forest and is one of the 25 global biodiversity hotspots (Myers et al. 2000), with over 3000 species of animals and plants (Yang et al. 2002). There are 24 villages and over 13,000 people living in the reserve. A large proportion (70%) of local population are ethnic minorities of Tujia and Miao. Current threats to ecosystems within FNNR are agriculture, forest fire, landslides, resource extraction, and illegal hunting, road construction, tourism development, and livestock grazing (Global Environment Facility 2004).

The GTGP was initiated in FNNR in 2000. Although slope steepness of farmlands is the main criterion for inclusion in GTGP in China (Liu et al. 2008), all farmlands in the reserve can be enrolled in GTGP regardless of steepness. Each participating household receives 3,583 yuan (or 520 US\$ at 1 US\$=6.89 yuan exchange rate in June, 2019) per ha of converted cropland per year. Once enrolled in GTGP, farmers can plant species described as ecological i.e., species that provide ecological functions and services like Chinese red pine (*Pinus massoniana*) and Chinese fir (*Cunninghamia lanceolata*), or plant species described as economic, i.e., a tea trees, fruit trees, and bamboo (*Phyllostachys heterocycla cv pubescens*). Farmers can also choose to let the forest regenerate without planting. To promote ecological benefits of GTGP, local government requires at least 80% of the tree plantings be ecological (Zhang 2003). Currently, about 55% of households in FNNR participate in GTGP, and the corresponding enrolled farmlands are in the experimental zone (areas outside the core zone boundary with elevations less than 2000 m, Fig. 1) of FNNR.

Vegetation and wildlife surveys

To investigate structure and species diversity of plants and wildlife, we measured forest type, understory and overstory plant cover, tree height and size (diameter breast height), and several metrics of biodiversity including understory, midstory, overstory plant richness and diversity, and wildlife species richness and occupancy in FNNR. We established 65 sampling plots (20 m×20 m), with 49 sites at natural forest and 16 sites at GTGP forest (Fig. 1). We classified forest type at these 65 plots based on established forest categories of the FNNR: evergreen broadleaf forest ($n=12$), mixed evergreen and deciduous forest ($n=27$), deciduous forest ($n=9$), bamboo ($n=6$), and afforested conifer ($n=11$).

For each plot, we recorded species of understory, midstory and overstory vegetation and estimated percentage of cover for each species. We calculated plant species richness and used percentage of cover as an estimate of abundance for each species to calculate Shannon's diversity index of understory, midstory and overstory vegetation. We measured DBH of tree with DBH>3 cm within 5 m radius from center and four corners of the plot and calculated maximum DBH, average DBH, and standard deviation of DBH for each plot. We used a range finder to visually estimate average tree height of the plot. We used a Nikon D7000 camera equipped with a Sigma 4.5 mm hemispherical lens to collect digital hemispherical photograph (DHP) at a minimum of five photo locations per plot to estimate canopy fractional cover (CFC), a measure for canopy closure defined as the percentage of tree canopy

area (Wang et al. 2005; Pueschel et al. 2012). We estimated percentage of understory cover at plots visually.

We deployed a Bushnell Trophy Cam infrared camera at each plot to monitor presence of mammals (>0.5 kg) and pheasants from April 2015 to August 2016. More details of vegetation and wildlife survey are provided in Supplementary (S1). Field efforts were conducted under permits from the San Diego State University's Institutional Animal Care and Use Committee (Protocol # 14-01-002L).

Data analysis

Our data analyses followed a stepwise approach to characterize differences in GTGP and natural forests. We first describe differences in forest cover, diversity measures of plant structure and composition using contingency analysis, *t*-tests and regression. To compare wildlife diversity, we used multi-species hierarchical occupancy modelling. Finally, we used correlation analysis to consider how strong a proxy canopy fractional cover served for ground-based diversity metrics related to structural and compositional diversity.

Forest cover, structure and diversity in GTGP and natural forest

We used contingency analysis to compare forest types between GTGP plots and natural forest sites. We used 2 tailed *t*-tests to compare CFC, average tree height, maximum DBH, average DBH, standard deviation of DBH, and percentage of understory cover between GTGP and natural forest sites. To account for effects of different observers on recording plant species, we used standard least square regression with individual observers as an independent variable in the model to test the difference in species diversity of understory, midstory and overstory vegetation between GTGP sites and natural forest sites. Poisson regression was used to test the difference in species richness (i.e. number of species) of understory, midstory and overstory vegetation.

Wildlife diversity in GTGP and natural forest

We used multi-species hierarchical occupancy modelling (Dorazio and Royle 2005) with a Bayesian approach (Rich et al. 2016) to estimate the probability a species occurred within the area sampled by a camera station during our survey period, while accounting for incomplete detection (MacKenzie et al. 2002). We treated each two-week period as a repeat survey at a particular camera station, resulting in an average of 17 (SE 1.1) surveys per camera station. We interpreted probability of occurrence of a species at a camera site as probability of using the habitat at the plot during the sampling period rather than consider the site to be occupied permanently (MacKenzie et al. 2006). We applied a generalized linear mixed modelling approach to incorporate site-level characteristics affecting species-specific occurrence and detection probabilities (Dorazio and Royle 2005; Russell et al. 2009).

We hypothesized the occurrence of wildlife may be influenced by canopy cover (CFC) and vegetation types (evergreen broadleaf forest [reference level], mixed evergreen and deciduous forest, deciduous forest, bamboo, and afforested conifer) and detection probability may be affected by presence of humans and dogs and distance to human disturbance. The occurrence probability for species was specified as:

$$\begin{aligned} \text{logit (probability of occurrence)} = & \alpha_0 + \alpha_1(\text{CFC}) + \alpha_2(\text{bamboo}) + \alpha_3(\text{conifer}) \\ & + \alpha_4(\text{mixed evergreen and deciduous}) + \alpha_5(\text{deciduous}), \end{aligned}$$

and detection probability as:

$$\begin{aligned} \text{logit (detection probability)} = & \beta_0 + \beta_1(\text{detection rate of humans and dogs}) \\ & + \beta_2(\text{distance to human disturbance}). \end{aligned}$$

We standardized all continuous covariates to have a mean of zero and standard deviation of one to help model convergence. Therefore, the inverse logit of α_0 and β_0 are the occurrence and detection probability, respectively at a camera station in evergreen broadleaf forest and with average covariate values. The remaining coefficients of continuous covariates (i.e. α_1 , β_1 and β_2) represent the effect of a one standard deviation increase in the covariate value.

We linked species-specific models to community models by treating species as random effects derived from community (Zipkin et al. 2010; Rich et al. 2016). Because wildlife species may react to environmental covariates differently as a function of animal type and body size, we divided wildlife into four groups based on animal type and mean body mass for males and females (Smith and Xie 2008). The four groups were pheasants, small (< 10 kg), medium (10–50 kg), and large (> 50 kg) mammals (Supplementary S2). We estimated overall species richness and richness by wildlife groups at each camera station. More information about the occupancy modeling and detailed specification for the group model and how we calculated species richness is presented in the Supplementary (S1). We used a 2-tailed *t*-test to compare mean estimated species richness of wildlife between GTGP sites and natural forest sites.

Correlation between CFC, forest structure, and species biodiversity

To assess whether CFC is a good proxy for forest structure and species diversity of wildlife and plants, we used Spearman rank-order correlation to test association between CFC and average tree height, maximum DBH, average DBH, standard deviation of DBH, understory, midstory, overstory plant species diversity and wildlife species richness.

Results

Forest cover, structure and diversity in GTGP and natural forest

Forest type at GTGP sites was significantly different from that at natural forest sites ($\chi^2(4, N=65)=45.54, p<0.001$; Fig. 2a). The most common forest type at natural sites was mixed evergreen deciduous forest (53%, $n=49$) while the most common forest type at GTGP plots was conifer (69%, $n=16$), which represented 0% at natural forest sites. Moreover, deciduous forest accounted for 18% at natural forest sites but was missing at GTGP sites. In general, overstory and understory cover were similar between GTGP plots and natural forest plots as CFC, average DBH, average tree height, and understory cover were not significantly different between GTGP and natural sites

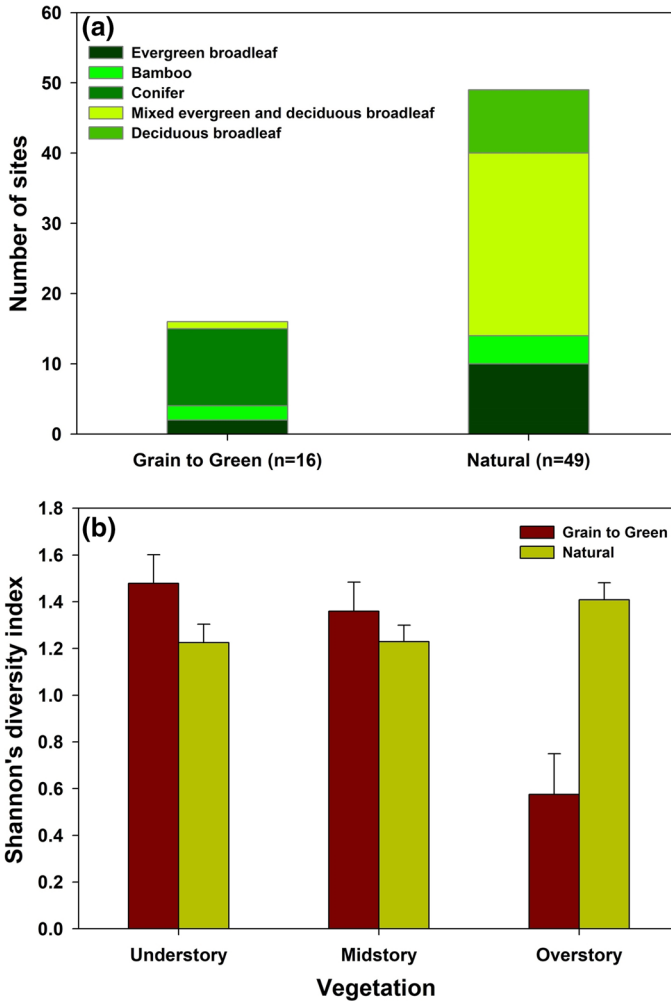


Fig. 2 Types of vegetation cover (a), and species diversity of understory, midstory, and overstory vegetation (b) at Grain-to Green forest and natural forest in Fanjingshan National Nature Reserve, China, 2015–2016

Table 1 Mean (\bar{x}), standard error (SE), and results of t tests of forest structure between Grain-to-Green (GTGP) forest and natural forest ($N=65$) in Fanjingshan National Nature Reserve, China 2015–2016

Variables	GTGP		Natural		t ratio	p value
	\bar{x}	SE	\bar{x}	SE		
Cover (CFC, %)	70.51	2.89	69.07	5.06	0.25	0.80
Average DBH (cm)	9.49	0.95	10.64	0.54	- 1.06	0.29
Maximum DBH (cm)	24.95	2.77	40.71	2.81	- 3.99	<0.001
Standard deviation of DBH (cm)	4.59	0.49	7.94	0.56	- 4.50	<0.001
Average tree height (m)	9.07	1.06	9.18	0.60	- 0.09	0.92
Understory cover (%)	31.60	6.60	28.60	3.80	0.38	0.70

(Table 1). However, there were fewer big trees and less variation in forest structure at GTGP sites, evidenced by lower maximum and standard deviation of DBH comparing to natural plots (Table 1). Diversity of understory and midstory vegetation was not significantly different between GTGP sites and natural sites after accounting for the effect of observer (understory: $F_{2,64} = 2.45$, $p = 0.09$; midstory: $F_{2,64} = 1.24$, $p = 0.30$; Fig. 2b). We also found species richness of understory ($\chi^2 = 1.9$, $p = 0.17$) and midstory vegetation ($\chi^2 = 0.73$, $p = 0.39$) were not significant between GTGP sites (understory: 4.9 species SE [0.34], midstory: 4.1 species SE [0.33]) and natural sites (understory: 3.5 species SE [0.25], midstory: 3.5 species SE [0.18]). Overstory plant diversity and richness were significantly lower at GTGP sites than at natural sites (diversity: $F_{2,64} = 15.39$, $p < 0.001$; richness: $\chi^2 = 17.38$, $p < 0.001$) after accounting for effect of observers. The diversity and species richness of overstory vegetation were 1.40 (SE 0.08) and 4.3 species (SE 0.22) respectively at natural sites while were 0.49 (SE 0.14) and 2.4 species (SE 0.44) respectively at GTGP sites (Fig. 2b).

Wildlife community in GTGP and natural forest

We detected 19 species of wildlife over 15,263 trap nights at 62 of 65 plots. Camera station-specific estimates of species richness ranged from 3 to 13 species (Supplementary S3), with a mean of eight species. Mean species richness was greater at natural sites (9 species SE [0.35]) than at GTGP sites (6 species SE [0.39]) ($t_{61} = -5.73$, $p < 0.001$, Fig. 3a). Comparing to evergreen broadleaf forest, mean species richness was lower in bamboo (5 species SE [0.82]) and coniferous forest sites (5 species SE [0.39]), and was highest in deciduous forest sites (10 species SE [0.48], Fig. 3b).

The mean probability of occurrence across all species and camera stations was 0.39 (SD 0.08, 95% CI 0.23–0.56), ranging from 0.11 for Grey snub-nosed monkey to 0.83 for wild boar (*Sus scrofa*). The mean detection probability across all species was of 0.11 (SD 0.02, 95% CI 0.07–0.16), ranging from 0.01 for Asian black bear to 0.4 for muntjac (Supplementary S2). Overall, CFC had no effects on probability of occurrence, but only Golden pheasant (*Chrysolophus pictus*) showed a negative effect (i.e. 95% CI does not overlap zero, Supplementary S2). At community level, probability of occurrence was lower at bamboo and coniferous forest comparing to at evergreen broadleaf forest, the reference level (Table 1). Comparing to evergreen broadleaf forest, seven of 19 species had higher probability of occurrence at mixed evergreen and deciduous forest, and three species had greater probability of occupancy at deciduous forest (Supplementary S2). Between GTGP sites and natural sites, three species had greater or equal to 0.5 of estimated occurrence probability at GTGP sites, including Elliot's pheasant (0.82 SE [0.08]), hog badger (*Arctonyx collaris*, 0.50 SE [0.11]), and wild boar (0.75 SE [0.05]), while probability of occurrence of eight species were > 0.5 at natural sites. Overall, species had lower detection probability in areas with presence of human and dogs, especially for large mammals (Table 2). Detection probability decreased as distance to human disturbance increased, and the association was greatest for medium mammals (Table 2). As expected, precision of estimates was lower for species with limited numbers of detections, leading to diffuse posterior distributions for their estimates of covariate effects. The Gelman–Rubin statistics indicated convergence for all parameters.

Fig. 3 Mean estimated wildlife species richness between Grain-to Green forest and natural forest (a), among forest types: bamboo, afforested conifer, evergreen broadleaf forest, mixed evergreen and deciduous forest, and deciduous forest (b), and in relation to canopy fractional cover in Fanjingshan National Nature Reserve, China, 2015–2016

CFC, forest structure and species biodiversity

CFC was positively correlated with average DBH ($r=0.34$, $p=0.004$), maximum DBH ($r=0.40$, $p=0.002$) and standard deviation of DBH ($r=0.45$, $p<0.001$). CFC was not correlated with average tree height ($r=0.20$, $p=0.3$). Among forest types, CFC was highest at bamboo (87% SE 2.2), following by evergreen broadleaf (79% SE 2.7), mixed evergreen deciduous (70% SE 4.0), and coniferous forest (67% SE 4.0), and was lowest at deciduous forest (46% SE 7.6). CFC was not correlated with either diversity ($r=-0.06$, $p=0.63$) or richness ($r=-0.02$, $p=0.87$) of overstory vegetation, as well as understory, midstory plant diversity and richness ($p>0.1$). CFC was negatively correlated with estimated wildlife species richness ($r=-0.38$, $p=0.003$, Fig. 3c).

Discussion

The GTGP program, like other PES programs, has been deemed to be a successful and effective land management strategy at improving some ecosystem services such as reducing soil erosion and surface runoff (Ouyang et al. 2016). With direct measurements of forest structure, plant and wildlife diversity, and occupancy of wildlife species, this study is one of the first to assess multiple ecological outcomes of PES program using several carefully chosen metrics of species and structural diversity. Our results suggest that PES programs, like GTGP, are associated with some measures of biodiversity benefits. In FNNR, we found understory and overstory plant cover, as well as understory and midstory plant diversity were comparable in GTGP and natural forest sites. Likewise, we found that reforested GTGP sites provided habitat for some species of interest in conservation, e.g., Elliot's pheasant (Chinese protected class I, IUCN Nearly Threatened) and hog badger (IUCN Vulnerable). Both findings suggest that, in addition to achieving the primary goals of reducing soil erosion and surface runoff, GTGP reforestation had some positive effects on biodiversity in FNNR.

However, there were important differences between GTGP forest and natural forest, particularly in the types of forest cover and heterogeneity of overstory vegetation. As a result, some biodiversity measures, such as plant overstory diversity and wildlife species richness, were significantly lower in GTGP forests than in natural forest. Recent PES research has flagged the need to develop reliable plant and animal diversity and function indicators, which can be used to measure, monitor, and assess the ecological outcomes of PES programs, improving PES program development and implementation (Barton et al. 2009; vonHaaren et al. 2012; Yin et al. 2013). Our analyses support this assertion as we found that an increase in forest canopy cover, a commonly used indicator of improved ecological conditions in the PES literature, was not a reliable proxy for increased floral or fauna diversity in FNNR.

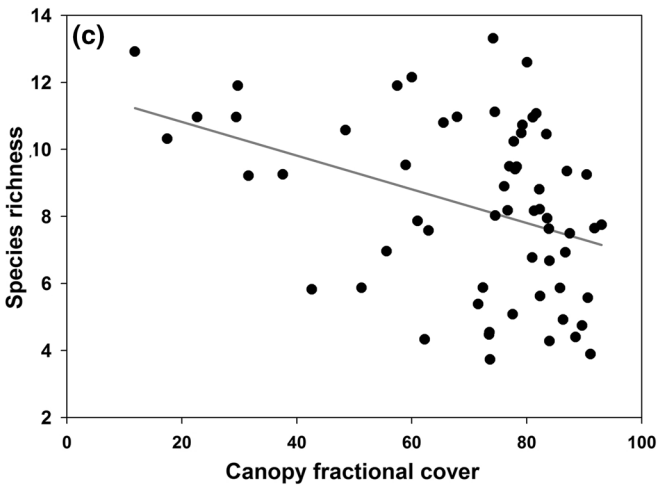
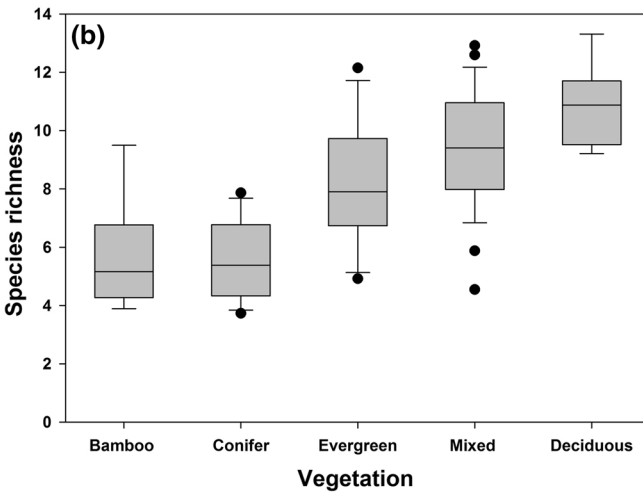
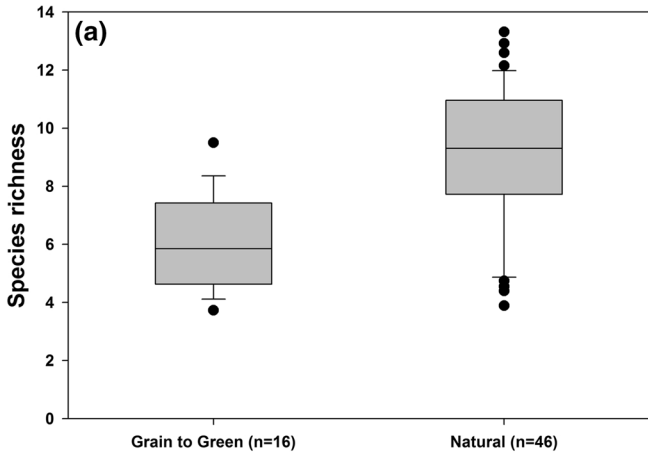


Table 2 Mean and 95% confidence interval estimates of the community-level and group-level hyper-parameters hypothesized to influence the probability of use (α) and detection (β) of 19 species of pheasants and mammals in Fajingshan National Nature Reserve, China 2015–2016

Variables	Community	Pheasant	Small mammal	Medium mammal	Large mammal
Cover ($\alpha 1$)	- 0.15 (- 0.50, 0.15)	- 0.62 (- 1.55, 0.14)	- 0.07 (- 0.88, 0.64)	0.01 (- 0.56, 0.54)	- 1.03 (- 3.50, 0.59)
Bamboo ($\alpha 2$)	- 1.05 (- 2.06 , - 0.12)	- 0.89 (- 3.40, 1.00)	- 1.50 (- 3.57, 0.32)	- 1.27 (- 3.21, 0.44)	3.92 (- 2.82, 19.49)
Conifer ($\alpha 3$)	- 1.31 (- 2.37 , - 0.43)	- 1.18 (- 3.84, 1.15)	- 1.32 (- 3.75, 1.28)	- 1.76 (- 4.32, 0.11)	1.06 (- 4.30, 16.91)
Mixed evergreen/deciduous ($\alpha 4$)	0.41 (- 0.15, 0.93)	1.21 (0.24 , 2.14)	- 0.85 (- 1.87, 0.09)	1.00 (0.18 , 1.87)	0.09 (- 1.61, 2.11)
Deciduous ($\alpha 5$)	0.50 (- 0.54, 1.64)	3.47 (0.80 , 8.73)	- 0.64 (- 2.86, 1.33)	0.32 (- 1.48, 2.15)	3.96 (- 3.82, 20.76)
Detection rate of human and dog ($\beta 1$)	- 0.11 (- 0.48, 0.22)	- 0.19 (- 0.60, 0.19)	0.37 (- 0.80, 1.58)	- 0.33 (- 3.63, 3.09)	- 4.29 (- 9.80 , -0.98)
Distance to human disturbance ($\beta 2$)	0.11 (- 0.10, 0.33)	0.10 (- 0.12, 0.32)	- 0.52 (- 3.24, 2.33)	- 1.97 (- 3.29 , - 0.63)	0.73 (- 0.25, 1.84)

Species groups included pheasants, small (<10 kg), medium (10–50 kg) and large (> 50 kg) mammals. Bold text indicates the 95% confidence interval does not overlap with zero

Influence of GTGP on plant and wildlife diversity

Although the primary goal of GTGP is to increase forest cover to mitigate soil erosion and runoff while providing residents economic benefits (Wandersee et al. 2012), other ecological outcomes including carbon sequestration, habitat restoration and supporting biodiversity have been identified as important outcomes for the PES program (Ouyang et al. 2016). While GTGP sites were found to have some diversity measures that were similar to natural forest sites, species, the diversity of tree and overstory species, planted at GTGP forest was low, and represented replacement rather than restoration as the planted species were not selected to represent the local forest (Liu et al. 2008). These differences are not unexpected and likely stem from the species used in GTGP forests including Chinese red pine, Chinese fir, and bamboo. Although bamboo and coniferous species (like pine and fir) are native in FNNR forests, GTGP forests are homogeneous and often not at the typical elevations where these species naturally occur (Yang et al. 2002). The lower diversity of overstory vegetation together with smaller tree size we observed at GTGP forest are also likely to be influenced by the expected successional dynamics (Huston and Smith 1987) and relatively short period since GTGP implementation (< 15 years).

Without a BACI design or counterfactual sites, it is challenging to directly measure how GTGP has affected any measure of floral or faunal diversity. However, given the empirical data on plant structure and diversity at GTGP sites, it is likely that some measures of plant and wildlife species richness have increased at GTGP sites since program implementation. Quantifying and characterizing these changes following PES implementation remains an important component of understanding the ecological impacts of GTGP, and other PES policy. Positive effects of PES on wildlife and wildlife habitat have been reported from several PES programs at other sites (Hua et al. 2016; Tuanmu et al. 2016; Basham et al. 2016). In our analysis of FNNR, we found wildlife species richness at GTGP forest was lower than at natural forest, although three wildlife species—Elliot's pheasants, hog badgers, and wild boars—were found to have a fairly high (> 0.5) probability of occurrence at GTGP sites. The lower wildlife species richness at GTGP forest was likely driven by the limited variation in forest type, structure and tree species at GTGP sites, and the relatively short time scale since program implementation. Wildlife was less likely to use bamboo and coniferous forest, which comprise of the majority of GTGP forest. For species that primarily use mixed evergreen and deciduous forests, like the Grey snub-nosed monkey (Niu et al. 2010), the GTGP, as currently implemented, does not provide necessary habitat. A recent study of GTGP forests in Sichuan Province, China also found that while this PES program provides some support for bird and bee diversity, diversity levels of both taxa were lower in GTGP sites than in natural forest (Hua et al. 2016). Beyond the direct influence of GTGP on habitat and species diversity, GTGP may confer indirect benefits to species biodiversity conservation by elevating awareness of human impacts on wildlife and conservation stewardship (Uchida et al. 2009; Wandersee et al. 2012).

Forest cover: an unreliable biodiversity proxy

Although canopy cover can be a key factor in predicting abundance or species richness of some groups of animals such as amphibians (Scheffers et al. 2014; Basham et al. 2016) and tree squirrels (Chen and Koprowski 2015), we found canopy fractional cover (CFC) was not a reliable proxy for many other ecological measures in FNNR. Although we found that CFC at GTGP forest was similar to CFC at natural forest, diversity of overstory vegetation

and wildlife species richness were not. CFC was highest in bamboo forest where wildlife species richness was lowest, and, conversely, CFC was lowest in deciduous forest where species richness was highest. This finding highlights the likely need for ecological monitoring beyond forest cover changes when considering positive co-benefits and ecological outcomes from PES programs. The recognition that CFC may not serve as a robust proxy for ecological metrics is important as GTGP has been suggested to increase biodiversity based on habitat quality models driven by land use and land cover (Hou et al. 2017). Our analyses in FNNR demonstrate that higher forest cover may not translate into higher plant or wildlife species biodiversity gains. Furthermore, using increase of forest cover as a proxy would overestimate the biodiversity conservation co-benefits provided by GTGP. The results from FNNR align with larger scale analyses in China. A national assessment of PES programs found that improvements in ecosystem services, such as increased forest cover, food production, and soil retention have been reported, but biodiversity-related habitat had decreased slightly (Ouyang et al. 2016).

Implications for PES programs and conclusions

In light of the pressing challenges to global ecosystems, there is a clear need for land management programs and policies to support both human well-being and ecological composition, process, and function (Scarano and Ceotto 2015). PES programs are an important management and land use instrument that aims to balance human and ecological well-being¹. By converting crop lands to forests, GTGP provides an important opportunities to reestablish forests in relatively short time periods (Yin and Yin 2010). However, GTGP forests are overwhelmingly monocultures across China (Liu et al. 2008; Hua et al. 2016), with only very few locations planted with native tree species similar to local natural forest. Although ecosystem services, like runoff and soil erosion reductions, are linked to increased forest cover, our findings and other research (e.g., Ouyang et al. 2016) suggest that canopy forest cover is not a good proxy for key ecological outcomes, such as species richness or structure. Evidence from FNNR, consistent with another case study in Sichuan Province (Hua et al. 2016), demonstrates that PES can provide modest improvements in some measures of species biodiversity. Yet, because PES programs like GTGP typically do not aim to restore vegetation communities to their original condition, the biodiversity gains by GTGP, as currently implemented, will likely be limited. As the Chinese government's commitment to ecosystem protection as a guiding vision, targeted changes to how GTGP sites are reforested is warranted (Wang et al. 2019). Sustainable and multi-purpose restored forests, i.e. forests that are managed for climate change mitigation, biodiversity conservation, and economic return, have been demonstrated to have the capacity to provide economically valuable resources like timber while also supporting species diversity (Nichols et al. 2006; Nölte et al. 2018). For example, use of native and mixed tree species, extension of rotation, reducing thinning, and conversion to uneven-aged forest have been shown increase biodiversity gains but may also generate other environmental and economic benefits such as carbon storage and tree harvesting (Hua et al. 2016; Nölte et al. 2018). Just as PES programs support multiple ecosystem services, there is a clear need to use multiple ecological metrics to evaluate and assess the ecological outcomes of PES programs. Our results demonstrate an opportunity to improve the return on PES investment through changes in program goals and implementation strategies so that PES can simultaneously support multiple ecosystem services.

Acknowledgements We acknowledge funding from the National Science Foundation under the Dynamics of Coupled Natural and Human Systems program (DEB-1212183), San Diego State University, and the equipment support by IDEA WILD. This project would not have been possible without the logistic support by Q. Xu and Z. Zhu of Yunnan University, W. Xu of the Chinese Academy of Sciences, and The Administration Office of Fanjingshan National Nature Reserve, especially D. F. Shia, D. C. Shia, and W. Dong. We thank staff, students, and volunteers of San Diego State University and Tongren College for assisting field work and processing data.

Data availability The datasets generated during and/or analysed during the current study are not publicly available due to sensitive information of critical endangered species, but may be available from the corresponding author on reasonable request.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References


- Balvanera P, Siddique I, Dee L et al (2014) Linking biodiversity and ecosystem services: current uncertainties and the necessary next steps. *Bioscience* 64:49–57. <https://doi.org/10.1093/biosci/bit003>
- Barton DN, Faith DP, Rusch GM et al (2009) Environmental service payments: evaluating biodiversity conservation trade-offs and cost-efficiency in the Osa Conservation Area, Costa Rica. *J Environ Manag* 90:901–911. <https://doi.org/10.1016/j.jenvman.2008.02.010>
- Basham EW, Gonzalez del Pliego P, Acosta-Galvis AR et al (2016) Quantifying carbon and amphibian co-benefits from secondary forest regeneration in the Tropical Andes. *Anim Conserv* 19:548–560. <https://doi.org/10.1111/acv.12276>
- Baylis K, Honey-ros J, Corbera E et al (2016) Mainstreaming impact evaluation in nature conservation. *Conserv Lett* 9:58–64. <https://doi.org/10.1111/conl.12180>
- Bremer LL, Farley KA, DeMaagd N et al (2019) Biodiversity outcomes of payment for ecosystem services: lessons from páramo grasslands. *Biodivers Conserv* 28:885–908. <https://doi.org/10.1007/s10531-019-01700-3>
- Brouwer R, Tesfaye A, Pauw P (2011) Meta-analysis of institutional-economic factors explaining the environmental performance of payments for watershed services. *Environ Conserv* 38:380–392. <https://doi.org/10.1017/S0376892911000543>
- Cardinale BJ, Duffy JE, Gonzalez A et al (2012) Biodiversity loss and its impact on humanity. *Nature* 489:326–326. <https://doi.org/10.1038/nature11373>
- Chen HL, Koprowski JL (2015) Animal occurrence and space use change in the landscape of anthropogenic noise. *Biol Conserv* 192:315–322. <https://doi.org/10.1016/j.biocon.2015.10.003>
- Daw TM, Hicks CC, Brown K et al (2016) Elasticity in ecosystem services: exploring the variable relationship between ecosystems and human well-being. *Ecol Soc* 21:11. <https://doi.org/10.5751/ES-08173-210211>
- Díaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16:646–655
- Dorazio RM, Royle JA (2005) Estimating size and composition of biological communities by modeling the occurrence of species. *J Am Stat Assoc* 100:389–398. <https://doi.org/10.1198/016214505000000015>
- Ferraro PJ, Kiss A (2002) Direct payments to conserve biodiversity. *Science* 298:1718–1719. <https://doi.org/10.1126/science.1078104>
- Global Environment Facility (2004) The management plan of Guizhou Fanjingshan National Nature Reserve. Sustainable Forestry Development Project and Protected Area Management.
- Harrison PA, Vandewalle M, Sykes MT et al (2010) Identifying and prioritising services in European terrestrial and freshwater ecosystems. *Biodivers Conserv* 19:2791–2821. <https://doi.org/10.1007/s10531-010-9789-x>

- Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol Lett* 8:23–29. <https://doi.org/10.1111/j.1461-0248.2004.00686.x>
- Hou Y, Lü Y, Chen W, Fu B (2017) Temporal variation and spatial scale dependency of ecosystem service interactions: a case study on the central Loess Plateau of China. *Landsc Ecol* 32:1–17. <https://doi.org/10.1007/s10980-017-0497-8>
- Hua F, Wang X, Zheng X et al (2016) Opportunities for biodiversity gains under the world's largest reforestation programme. *Nat Commun* 7:12717. <https://doi.org/10.1038/ncomms12717>
- Huston M, Smith T (1987) Plant succession: life history and competition. *Am Nat* 130:168. <https://doi.org/10.1086/284704>
- IPBES (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.
- Jack BK, Kousky C, Sims KRE (2008) Designing payments for ecosystem services: lessons from previous experience with incentive-based mechanisms. *Proc Natl Acad Sci USA* 105:9465–9470. <https://doi.org/10.1073/pnas.0705503104>
- Kareiva P, Marvier M (2012) What is conservation science? *Bioscience* 62:962–969. <https://doi.org/10.1525/bio.2012.62.11.5>
- Kareiva P, Watts S, McDonald R, Boucher T (2007) Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science* 316:1866–1869. <https://doi.org/10.1126/science.1140170>
- Lewison RL, An L, Chen X (2017) Reframing the payments for ecosystem services framework in a coupled human and natural systems context: strengthening the integration between ecological and human dimensions. *Ecosyst Heal Sustain* 3:5
- Liu J (2003) Protecting China's biodiversity. *Science* 300:1240–1241
- Liu J, Li S, Ouyang Z et al (2008) Ecological and socioeconomic effects of China's policies for ecosystem services. *Proc Natl Acad Sci USA* 105:9477–9482. <https://doi.org/10.1073/pnas.0706436105>
- Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol Evol* 27:19–26. <https://doi.org/10.1016/J.TREE.2011.08.006>
- MacKenzie DI, Nichols JD, Lachman GB et al (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255. <https://doi.org/10.2307/3072056>
- MacKenzie DI, Nichols JD, Royle JA et al (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier Academic Press, London
- Mathieu L, Tinch R, Provins A (2018) Catchment management in England and Wales: the role of arguments for ecosystems and their services. *Biodivers Conserv* 27:1639–1658. <https://doi.org/10.1007/s10531-016-1176-9>
- Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: biodiversity synthesis. Washington, DC
- Miller B, Soulé ME, Terborgh J (2014) 'New conservation' or surrender to development? *Anim Conserv* 17:509–515. <https://doi.org/10.1111/acv.12127>
- Miteva DA, Pattanayak SK, Ferraro PJ (2012) Evaluation of biodiversity policy instruments: what works and what doesn't? *Oxford Rev Econ Policy* 28:69–92. <https://doi.org/10.1093/oxrep/grs009>
- Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858. <https://doi.org/10.1038/35002501>
- Naeem S, Ingram JC, Varga A et al (2015) Get the science right when paying for nature's services: few projects adequately address design and evaluation. *Science* 347:1206–1207. <https://doi.org/10.1126/science.aaa1403>
- Newbold T, Hudson LN, Arnell AP et al (2016) Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science* 353:288–291. <https://doi.org/10.1126/science.aaf2201>
- Nichols JD, Bristow M, Vanclay JK (2006) Mixed-species plantations: prospects and challenges. *For Ecol Manage* 233:383–390. <https://doi.org/10.1016/j.foreco.2006.07.018>
- Niu K, Tan CL, Yang Y (2010) Altitudinal movements of Guizhou Snub-Nosed Monkeys (*Rhinopithecus brelichi*) in Fanjingshan National Nature Reserve, China: implications for conservation management of a flagship species. *Folia Primatol* 81:233–244. <https://doi.org/10.1159/000322115>
- Nölte A, Meilby H, Yousefpour R (2018) Multi-purpose forest management in the tropics: Incorporating values of carbon, biodiversity and timber in managing *Tectona grandis* (teak) plantations in Costa Rica. *For Ecol Manage* 422:345–357. <https://doi.org/10.1016/J.FORECO.2018.04.036>
- Ouyang Z, Zheng H, Xiao Y et al (2016) Improvements in ecosystem services from investments in natural capital. *Science* 352:1455–1459. <https://doi.org/10.1126/science.aaf2295>
- Prager CM, Varga A, Olmsted P et al (2016) An assessment of adherence to basic ecological principles by payments for ecosystem service projects. *Conserv Biol* 30:836–845. <https://doi.org/10.1111/cobi.12648>

- Pueschel P, Buddenbaum H, Hill J (2012) An efficient approach to standardizing the processing of hemispherical images for the estimation of forest structural attributes. *Agric For Meteorol* 160:1–13. <https://doi.org/10.1016/j.agrformet.2012.02.007>
- Quijas S, Romero-Duque LP, Trilleras JM et al (2019) Linking biodiversity, ecosystem services, and beneficiaries of tropical dry forests of Latin America: review and new perspectives. *Ecosyst Serv* 36:100909. <https://doi.org/10.1016/j.ECOSER.2019.100909>
- Rich LN, Miller DAW, Robinson HS et al (2016) Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. *J Appl Ecol* 53:1225–1235. <https://doi.org/10.1111/1365-2664.12650>
- Russell RE, Royle JA, Saab VA et al (2009) Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. *Ecol Appl* 19:1253–1263. <https://doi.org/10.1890/08-0910.1>
- Scarano FR, Ceotto P (2015) Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. *Biodivers Conserv* 24:2319–2331. <https://doi.org/10.1007/s10531-015-0972-y>
- Scheffers BR, Edwards DP, Diesmos A et al (2014) Microhabitats reduce animal's exposure to climate extremes. *Glob Change Biol* 20:495–503. <https://doi.org/10.1111/gcb.12439>
- Smith AT, Xie Y (2008) A guide to the mammals of China. Princeton University Press, Princeton
- Tuanmu MN, Viña A, Yang W et al (2016) Effects of payments for ecosystem services on wildlife habitat recovery. *Conserv Biol* 30:827–835. <https://doi.org/10.1111/cobi.12669>
- Uchida E, Rozelle S, Xu J (2009) Conservation payments, liquidity constraints, and off-farm labor: impact of the Grain-for-Green Program on rural households in China. *Am J Agric Econ* 91:70–86. <https://doi.org/10.1111/j.1467-8276.2008.01184.x>
- vonHaaren C, Kempa D, Vogel K, Rüter S (2012) Assessing biodiversity on the farm scale as basis for ecosystem service payments. *J Environ Manage* 113:40–50. <https://doi.org/10.1016/j.jenvman.2012.07.033>
- Wandersee SM, An L, López-Carr D, Yang Y (2012) Perception and decisions in modeling coupled human and natural systems: a case study from Fanjingshan National Nature Reserve, China. *Ecol Modell* 229:37–49. <https://doi.org/10.1016/j.ecolmodel.2011.08.004>
- Wang C, Qi J, Cochrane M (2005) Assessment of tropical forest degradation with canopy fractional cover from Landsat ETM+ and IKONOS imagery. *Earth Interact* 9:1–18. <https://doi.org/10.1175/EI1133.1>
- Wang C, Ouyang H, Maclaren V et al (2007) Evaluation of the economic and environmental impact of converting cropland to forest: a case study in Dunhua county, China. *J Environ Manage* 85:746–756. <https://doi.org/10.1016/j.jenvman.2006.04.025>
- Wang X, Hua F, Wang L et al (2019) The biodiversity benefit of native forests and mixed-species plantations over monoculture plantations. *Divers Distrib*. <https://doi.org/10.1111/ddi.12972>
- World Bank (2001) The World Bank China: air, land, and water. World Bank, Washington DC
- Wu G, Wang H, Fu H et al (2004) Habitat selection of Guizhou golden monkey (*Phinopithecus roxellanae brelichi*) in Fanjing Mountain Biosphere Reserve, China. *J For Res* 15:197–202
- Wu J, Zhao Y, Yu C et al (2017) Land management influences trade-offs and the total supply of ecosystem services in alpine grassland in Tibet, China. *J Environ Manage* 193:70–78. <https://doi.org/10.1016/j.jenvman.2017.02.008>
- Wunder S (2007) The efficiency of payments for environmental services in tropical conservation. *Conserv Biol* 21:48–58. <https://doi.org/10.1111/j.1523-1739.2006.00559.x>
- Wunder S (2013) When payments for environmental services will work for conservation. *Conserv Lett* 6:230–237. <https://doi.org/10.1111/conl.12034>
- Xu J, Yin R, Li Z, Liu C (2006) China's ecological rehabilitation: Unprecedented efforts, dramatic impacts, and requisite policies. *Ecol Econ* 57:595–607. <https://doi.org/10.1016/j.ecolecon.2005.05.008>
- Yang Y, Lei X, Yang C (2002) Ecology of the wild Guizhou snub-nosed monkey (*Rhinopithecus bieti*). Guizhou Science and Technology Press, Guiyang
- Yin R, Yin G (2010) China's primary programs of terrestrial ecosystem restoration: initiation, implementation, and challenges. *Environ Manage* 45:429–441
- Yin R, Liu T, Yao S, Zhao M (2013) Designing and implementing payments for ecosystem services programs: lessons learned from China's cropland restoration experience. *For Policy Econ* 35:66–72. <https://doi.org/10.1016/j.forpol.2013.06.010>
- Zhang H (2003) Guidance and practice of converting cropland to forest. Chinese Press of Agricultural Science and Technology, Beijing, pp 3–120
- Zipkin EF, Andrew Royle J, Dawson DK, Bates S (2010) Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biol Conserv* 143:479–484. <https://doi.org/10.1016/j.biocon.2009.11.016>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Affiliations

Hsiang Ling Chen¹  · Rebecca L. Lewison² · Li An³ · Yu Hsin Tsai³ · Douglas Stow³ · Lei Shi⁴ · Shuang Yang³

✉ Hsiang Ling Chen
hsiangling@dragon.nchu.edu.tw

¹ Department of Forestry, National Chung Hsing University, 145, Xingda Rd., Taichung 402, Taiwan

² Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182-4614, USA

³ Department of Geography, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182-4493, USA

⁴ Fanjingshan National Nature Reserve Administration, 17 Sanxing West Rd., Shuangjiang Township, Jiangkou, Guizhou Province, China