



Plantation vs. natural forest: Matrix quality determines pollinator abundance in crop fields

Hisatomo Taki¹, Yuichi Yamaura², Kimiko Okabe¹ & Kaoru Maeto³

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Correspondence and
requests for materials
should be addressed to
H.T. (htaki@affrc.go.
ip)

¹Department of Forest Entomology, Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan, ²Division of Environmental Resources, Graduate School of Agriculture, Hokkaido University, Nishi 9 Kita 9, Kitaku, Sapporo, Hokkaido 050-8589, Japan, ³Laboratory of Insect Science, Graduate School of Agricultural Science, Kobe University, Rokkodai, Nada, Kobe, Hyogo 657-8501 Japan.

In terrestrial ecosystems, ecological processes and patterns within focal patches frequently depend on their matrix. Crop fields (focal patches) are often surrounded by a mosaic of other land-use types (matrix), which may act as habitats for organisms and differ in terms of the immigration activities of organisms to the fields. We examined whether matrix quality affects wild pollinator abundance in crop fields, given that the species (*Apis cerana*) generally nest in the cavities of natural trees. We examined fields of a pollination-dependent crop surrounded by plantations and natural forests, which comprised the matrix. Our analysis revealed a clear positive effect of the natural forest on the pollinator abundance, but the plantation forest had little effects. These indicate that agricultural patches are influenced by their matrix quality and the resulting crop pollinator abundance, suggesting the importance of matrix management initiatives such as forest restoration surrounding agricultural fields to improve crop production.

In terrestrial ecosystems, ecological processes and patterns within focal patches frequently depend on their dominant matrix^{1–3}. Crop fields (focal patches) are often surrounded by a mosaic of other land use types (matrix), which may act as habitats for organisms and differ in terms of the immigration activities of organisms to the fields⁴. Both theoretical and empirical studies have shown that improving the quality of the surround land use types enhances biodiversity as well as a range of ecosystem functions provided by different species in agro-ecosystems^{5,6}. For example, a heterogeneous landscape comprising a matrix of semi-natural or natural land cover alternating with agricultural land generally has a greater biodiversity than a homogeneous landscape⁷.

Of the world's terrestrial surfaces, forests comprise the largest proportion of semi-natural or natural land, occupying approximately 30% of the total land area worldwide⁸. In some countries, plantations account for a large proportion of forest area. For example, 12% of the land cover in the UK consists of forest, with 68% of the forest area being plantation, while in Japan, 68% of the land area is covered by forest, with 42% of that being plantation⁸. Plantation forests, typically consisting of one or a few tree species, are grown as even-aged monocultures, intensively managed, and harvested on relatively short rotations. These characteristics raise concerns that plantation forests may negatively impact forest biodiversity⁹. It is also possible for plantation forests, depending on the specific management practices and region, to play a role in conserving biodiversity¹⁰. However, for example, the multiple taxa in tropical forests in the Amazon demonstrate that plantation forests are often less diverse than natural forests¹¹.

Animal pollinators are essential providers of crop pollination services¹². Several crop pollinator species depend on forests for their food and nest resources, as seen in both temperate and tropical regions (e.g.^{13,14}). One such important forest-dependent pollinator species in Asia is *Apis cerana*, which is widespread in temperate and tropical countries¹⁵ and plays important roles in crop pollination services therein¹⁶. This generalist honeybee species contributes to the pollination of a variety of crops, including apple¹⁷, cauliflower, cabbage¹⁸, radish¹⁹, litchi²⁰ and cardamom²¹. Wild populations of *A. cerana* are highly dependent on forests for nesting and food resources, given that they mainly nest in tree cavities^{22,23} and collect pollen and nectar from various species of trees in temperate and tropical regions^{24,25}. Therefore, monocultured, even aged plantation forests that are intensively managed and harvested on relatively short rotations, might limit the available habitat of *A. cerana*.

The main goal of this study was to examine whether the quality of a forested matrix affects the abundance of *A. cerana* in a crop field in central Japan. We examined an agro-ecosystem of buckwheat (*Fagopyrum esculentum*)



Table 1 | Deviance information criteria (DIC) of 64 models with different areas of natural and plantation forests.

	Plantation									
	500m	1000m	1500m	2000m	2500m	3000m	3500m	4000m	mean	
500m	4.99	2.57	3.77	4.17	4.73	4.5	4.86	5.18	4.35	
1000m	3.3	1.49	1.37	1.41	1.79	1.8	0.98	1.4	1.69	
1500m	1.19	0.77	0.55	0*	0.8	0.67	1.14	1.5	0.83	
2000m	1.75	1.52	2.27	0.58	1.87	2.46	3.58	4	2.25	
Natural forest	2500m	2.36	2.72	3.36	2.52	3.22	3.41	4.15	4.43	3.27
	3000m	2.92	3.34	4.49	5.29	4.74	4.16	4.65	5	4.32
	3500m	3.76	2.07	4.85	5.21	5.36	4.62	5.23	4.87	4.5
	4000m	5.76	1.2	4.07	6.23	6.27	5.94	6.09	6.11	5.21
mean	3.25	1.96	3.09	3.17	3.6	3.45	3.84	4.06		

Models whose DIC differences to the best model (DIC = 0.0) smaller than 2.0 were highlighted by grey. *Used in parameter estimation.

surrounded by conifer plantations and natural broad-leaved forests as the matrix. The crops in this region are pollinated by wild insect species, including a native honeybee (*A. cerana*), and a managed introduced honeybee (*A. mellifera*)²⁶. After examining this system for three years, we predicted that the abundance of *A. cerana* in the buckwheat fields would show a stronger positive correlation with the total area of surrounding natural forests compared to that of surrounding plantation forests²⁷. Here, we tested this prediction and analyzed the potentially negative influence of the presence of *A. mellifera* on the abundance of *A. cerana*. *A. mellifera* is a domesticated and dominant managed honeybee in the study region. No wild populations of *A. mellifera* have yet been reported in mainland Japan. It is suspected that *A. mellifera* has been unable to establish wild populations in part due to the presence of the Asian giant hornet (*Vespa mandarinia*), the only known hornet species to have evolved mass predation of other social bees and wasps, whereas *A. cerana* possesses a unique thermal defense against these hornets²⁸.

Results

The deviance information criteria (DICs) were lowest for the models incorporating the area of natural and plantation forests at 1500-m and 2000-m scales, respectively (Table 1). The model with the area of natural forest set at a 1000–1500-m scale and that with the plantation forest area set at a 1000–2500-m scale were well supported. We then used the best-fit model to estimate the effects of the three covariates (the abundance of *A. mellifera* and the areas of natural and plantation forests) on the abundance of *A. cerana*. The values of \hat{R} for all estimated values were less than 1.01 (Table 2; Supplementary Table S1) indicating that this model was well converged²⁹. The results showed that the effect of natural forest was significant and that those of the plantation forest and *A. mellifera* were not significant (Table 2),

although the areas of surrounding natural and plantation forests positively affected the abundance of *A. cerana*, while the presence of *A. mellifera* showed a negative effect. Random year effects indicated that *A. cerana* was most abundant in the third year, and the lowest population numbers were observed in the second year. Spatial random effects showed that sites within 1 km were positively correlated (Fig. 1).

Discussion

Foraging distance of pollinator species is one key factor to influence the spatial scale of certain landscape factors^{30,31}. The abundance of *A. cerana* in the crop fields was most strongly correlated with the area of natural forest in the matrix within the 1500-m scale. The wild honeybee species nests in cavities of tree species that are mainly found in forests²², and uses the flower resources of various forest tree, shrub and herb species for food²⁴. Thus, forests provide nest resources (cavities) as well as food resources (flowers)³². These resources are relatively fewer in the plantation forests, where the main species of planted conifers are *C. japonica* and *C. obtusa*. Plantation trees are carefully managed and do not provide the types of cavities that are preferred as nesting sites for the wild honeybees. Indeed, previous studies have revealed that tree cavities and understory vegetation are more available in natural forests than in conifer plantations that are grown as even-aged monocultures and are usually harvested on relatively short rotations^{33,34}.

Although the influence was little, analysis of the relationship between the abundances of *A. cerana* and *A. mellifera* showed that their abundances were negatively related, which could be caused by, for example, competition for limiting resources. Taki et al.²⁷ reported a negative correlation between the abundances of *A. cerana* and of *A. mellifera* based on two years of observations of buckwheat flowers in the same study region. Additionally, Nagamitsu & Inoue²⁴ compared pollen sources for *A. cerana japonica* and *A. mellifera* in a primary beech forest in Honshu, Japan. They found that most pollen sources were shared between the two honeybee species and that seasonal variation in the pollen utilization of the two honeybees was similar. These results suggest that there may be some conflict between the two honeybee species, although further research on resource use and behavioral competition for buckwheat flowers between the two bee species is necessary.

In summary, *A. cerana* abundance showed a relatively strong positive correlation with the natural forest matrix compared to the plantation matrix. Thus, replacing natural forest with plantation might have adverse effects on biodiversity conservation and restoration³⁵. Possible approaches to forest management in a plantation-dominated landscape may include natural regeneration and retention of original native trees¹⁰. In the case of Japan, where 68% of land is covered by forest and 42% of which comprises plantations of mainly coniferous species⁸, public demand for the re-establishment of native broadleaved

Table 2 | Estimates of the relevant model parameters in the best-fit spatial regression model.

Variable	Range of estimates*			\hat{R}
	2.5%	50%	97.5%	
year[1]	-1.00	0.14	1.44	1.00
year[2]	-1.72	-0.54	0.72	1.00
year[3]	-0.70	0.42	1.69	1.00
$\alpha_{\text{intercept}}$	-0.13	1.32	2.58	1.00
$\alpha_{\text{mellifera}}$	-0.37	-0.18	0.01	1.00
$\alpha_{\text{nat_for}}$	0.60	1.11	1.71	1.00
$\alpha_{\text{plant_for}}$	-0.15	0.18	0.53	1.00
τ	0.93	3.92	12.82	1.00
ϕ	0.18	1.01	4.65	1.00

*Shown in percentile.

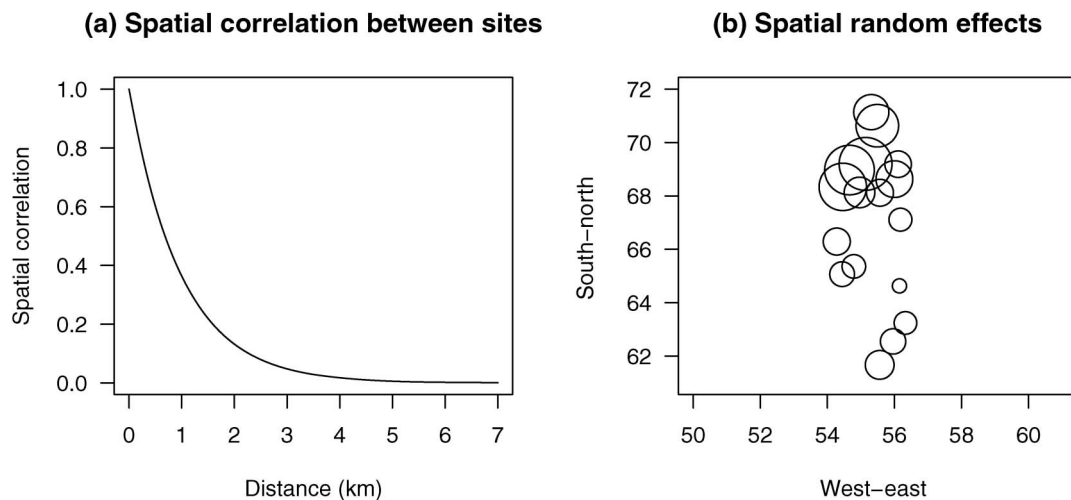


Figure 1 | Spatial effects modeled by the spatial regression model. (a) Spatial correlation was depicted using the spatial decay function: $\exp[-(\phi d_{ij})]$, where $\phi = 1.01$ (estimated median value). (b) Spatial random effects of each site are indicated by relative circle size.

species has been increasing³⁶. Such public involvement must take place in developed and developing countries that continue to practice afforestation. Initiatives to restore monoculture plantations to naturally regenerated forests would initiate positive feedbacks for forest dependent organisms, which may act as ecosystem service providers in agricultural ecosystems.

The patch/matrix dichotomy is a broad oversimplification for many species in human-altered landscapes; however, improving the quality of matrix contexts will likely result in improved species conservation³⁷. Therefore, the recognition and consideration of how to manage matrices when making land use decisions is important for the future of the world's terrestrial ecosystems^{38,39}. Our results indicate that land management that includes focal agricultural fields and surrounding land use types is important to improving crop yields, and that forest management can contribute to improving agriculture.

Methods

Study region and crops. The study was conducted in the mountainous region of Hitachiota, Ibaraki Prefecture, central Japan (36°30'–36°40' N, 140°23'–140°31' E). Landscapes in the study region consist of agricultural fields (buckwheat fields, paddies, orchards, and tea fields), with the dominant surrounding semi-natural to natural lands comprising cedar plantations and deciduous forests. The original dominant canopy species in the forested areas were deciduous broad-leaved trees such as konara oak (*Quercus serrata*), mizunara oak (*Quercus crispula*) and Japanese beech (*Fagus crenata*), and the main species in the conifer plantations are Japanese cedar (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*)⁴⁰.

Buckwheat is a characteristic crop grown by small local landholders in the region. We conducted a field study over three consecutive years, with 15 field sites examined in 2007 and 2009 and two additional sites in 2008 for a total of 17 sites. The timing of sowing and harvesting is similar in all fields across the region. The sowing of each field is typically completed during the second week of August, and harvesting takes place in mid October. Consequently, the blooming time of each study site was synchronized. No fertilizers, pesticides, or other agrochemicals are used in these fields.

Insect samplings. We sampled *A. cerana* and *A. mellifera* visiting the flowers of common buckwheat for food resources (both pollen and nectar) on sunny days during the blooming period in September (Fig. 2). In each buckwheat field, we used insect nets to capture honeybees visiting flowers within a 1.5 × 1.5-m quadrat approximately 2 m in from the southern edge of the field to standardize sampling among the field sites. In each field, all insects visiting flowers were sampled for 15 min between 9:00 and 12:00. This method was based on previous examinations of flower-visiting insects and pollen availability at different times of the day^{41–43}. A single person (H. T.) conducted the samplings, which included three trials of 15 min each for each study field between 9:00 and 12:00, and the order of each trial was randomized.

Forested matrix. We measured the areas of tree plantations and natural forests surrounding the study crop sites at radii of 500, 1000, 1500, 2000, 2500, 3000, 3500, and 4000 m from the centers of sampling points in the study fields. The radii were selected based on the reported foraging ranges of *A. cerana*⁴⁴. The tree plantation and natural forest areas were delineated from a 1:50,000 digital vegetation map published by the Ministry of the Environment of Japan in 1999. This vegetation map was

updated with more recent large-scale deforestations and land-use changes through the interpretation of 2.5-m spatial resolution panchromatic SPOT 5 satellite imagery (Spot Image, Toulouse, France) in 2004 using ArcGIS 9.2 software (ESRI Inc., Redlands, CA, USA).

Data analysis. We examined the effects of three covariates (the abundance of *A. mellifera* and the areas of natural and plantation forests) on the abundance of *A. cerana* as a response variable over three years under a Bayesian framework using WinBUGS Ver. 1.4.3⁴⁵, R2WinBUGS Ver. 2.1–13⁴⁶, and R Ver. 2.10.1⁴⁷. We assumed the abundance of *A. cerana* to be a Poisson-distributed variable and used a log-link function. Year was used as a random effect (i.e. year_{*i*}, *i* = 1, 2, 3), and the three covariates as simple linear terms. Given that we used spatial sampling data, it was necessary to consider spatial autocorrelation among sites (e.g.⁴⁸). Thus, we used a random site variable as an additional covariate (site_{*j*}, *j* = 1, ..., 17) using a Bayesian Gaussian kriging model⁴⁹ with GeoBUGS Ver. 1.2⁵⁰. Following Thomas et al.⁵⁰, we centered the mean for each site to zero ($\mu = 0$) using a hierarchically centered model. In this spatial model, between-area correlation is modeled using an exponential decay function: $\exp[-(\phi d_{ij})^\kappa]$, where d_{ij} is distance between sites *i* and *j*, ϕ is the rate of decline of correlation with distance, and κ is set to 1⁵⁰. We used uninformative vague priors for estimated parameters⁵¹: year_{*i*} ~ Norm(0, var_{year}); 1/var_{year} ~ Gamma(0.001, 0.001); α ~ Norm(0, 1000); ϕ ~ Uniform(0.15, 5); site_{*j*} ~ Norm(0, var_{site}); 1/var_{site} ~ Gamma(0.001, 0.001), where α is the intercept and estimates the three covariates (i.e. the slope of a simple term), var_{site} is the variation of random site effects (inverse of var_{site} is called τ). For the sites surveyed in only 1 or 2 years, the abundance of *A. cerana* in unsampled years was defined as NA, and the abundance of *A. mellifera* was replaced with the average value of 5.7⁵². The range of ϕ was chosen such that the between-site correlation was within [0, 0.47] at 5 km. The three covariates were standardized before the analysis. We ran three simulations of 100,000 iterations with different initial values,



Figure 2 | Wild honeybees (*Apis cerana*) visiting buckwheat flowers (*Fagopyrum esculentum*).



discarded the first 1000 and thinned by 50. This process was conducted with eight different radii of natural and plantation forest areas, producing a total of 8×8 models, which were compared using deviance information criteria (DICs)⁵¹.

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Author contributions

HT, YY, KO and KM conceived the experiments. HT and YY designed the study, analyzed the data, and wrote the main manuscript text. HT performed the experiments. All authors reviewed the manuscript.

Additional information

Supplementary information accompanies this paper at <http://www.nature.com/scientificreports>

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