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# The species richness/abundance–area relationship of bees in an early successional tree plantation

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## Abstract

Animal pollination is a vital ecosystem service, and wild bees are essential providers of this service for both crops and wild flowering plants. The early successional stage of a plantation, which can be dominated by grasses and herbaceous plant species, can provide a habitat for various species of wild bees. We sampled bees from 13 early successional plantation patches of different sizes, ranging from 1.3 to 10 ha. We then applied a hierarchical community model to infer species richness/abundance–area relationships. The results showed that estimates of population densities of individual species were unchanged with respect to area, suggesting that smaller patches can have the same value per area as larger patches. Estimated species richness increased rapidly for the small range of patch sizes examined. Total abundance was found to linearly increase with area. The inclusion of random site effects into the model resulted in significant density variations among patches; therefore, patch area was not the only determining factor of species abundance. These outcomes in relation to management operations for forests and plantations suggest that small patches of early successional forest contribute to conserve and restore wild bee diversity.



***Keywords:*** *Larix leptolepis*; Planted; Clear-cut; Succession; Apoidea; Anthophila; Apiformes; Hymenoptera; Species-area

## Introduction

Animal pollination is a vital ecosystem service (Millennium Ecosystem Assessment, 2005), and wild bees are essential providers of this service as they are important pollinators of the majority of crops and wild flowering plants (Michener, 2007). The estimated proportion of flowering plants pollinated by animals, including wild bees, exceeds 85% worldwide (Ollerton, Winfree, & Tarrant, 2011). Pollinators also increase the production of about 75% of the most widely planted crops worldwide (Klein et al., 2007), which have an estimated annual economic value of $235–577 billion (IPBES, 2016). In some parts of the world, the diversity and abundance of wild bees have decreased, leading to concern about habitat degradation and a crisis of pollination services (Potts et al., 2010). To maintain such services, it is important to conserve and restore forests and grasslands as appropriate habitats for wild bees to conserve their high abundance and species richness in these natural and semi-natural habitats (Dicks et al., 2016).

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Forests are important natural and semi-natural terrestrial ecosystems, and natural disturbances and forest management operations within these ecosystems can create suitable habitats for wild bees. Both natural and human disturbances often drive the regeneration of forests, which leads to a succession in plant communities, affecting animals (Horn, 1974). Studies have demonstrated that different species prefer specific successional stages and the diversity of various taxa peaks at different times as succession proceeds (Spies & Turner, 1999). The early successional stages of forests can be dominated by grasses and herbaceous plant species because tree canopies often do not dominate the forests. These provide open ground and rich understory plant communities as resources which attract and sustain the diversity of pollinator taxa (Hanula, Ulyshen, & Horn, 2016; Swanson et al., 2011). This tendency has been reported for numerous species of wild bees, implying that the creation of open areas after harvest or natural disturbance in forests or in forests with very low basal areas can contribute to the conservation and restoration of habitats for wild bee species(Hanula, Horn, & O'Brien, 2015; Taki, Okochi et al., 2013).

The idea that the number of species increases with area, namely, the species richness–area relationship (SAR), is one of the few broadly accepted laws in ecology (Lawton, 1999). Although still debated, various mechanisms have been proposed to explain this general pattern. Because larger habitats typically have larger population sizes compared with smaller areas, larger areas tend to have higher species richness (number of species with at least one individual). This is a concise explanation of SARs determined by random placement models (Coleman, Mares, Willig, & Hsieh, 1982; Williams, 1995), and holds unless population densities of individual species greatly decrease with area (Yamaura, Connor, Royle, Itoh, Sato, Taki, et al., 2016). Deviations from constant densities, such as positive density–area relationships (Bender, Contreras, & Fahrig, 1998; Connor, Courtney, & Yoder, 2000) can affect the form of SARs and have important implications from an application perspective.

Therefore, this study examined the relationships between population densities of individual species comprising communities of bees (Hymenoptera: Apoidea: Anthophila) and the area of early-successional plantation patches. The overall objective of this study was to model SAR and species abundance–area relationship (AAR) based on density–area relationships. Because we could not survey the total area of the patches, we used the framework of a hierarchical community model (HCM) to account for spatial incompleteness in the field sampling (Yamaura, Connor, et al., 2016Yamaura, Connor, Royle, Itoh, Sato, Taki, et al., 2016). HCM treats communities as ensembles of individual species and constructs models of rare species by borrowing information from common species (Ovaskainen & Soininen, 2011). This is a great benefit in accounting for species richness in communities where rare species can play important roles (Dorazio, Royle, Soderstrom, & Glimskar, 2006), and provides the underlying species-level mechanisms of community-level SAR and AAR. These outcomes should help to identify effective management operations for forests and plantations to conserve and restore bee diversity in early successional plantation forest.

## Materials and methods

### Study sites

The study region was in the eastern Tokachi plain, located in Urahoro and Ikeda, Hokkaido (approximately 20 × 30 km, 42°54′N, 143°36′E) (Yamaura, Connor, Royle, Itoh, Sato, Taki, et al., 2016). This area is mainly covered by forest, but the valleys and southernmost areas are used for agriculture (pasture and arable fields). Forest management operations are active in this area, especially in larch (*Larix leptolepis*) plantations. We selected 13 early successional plantation patches, ranging in size from 1.3 to 10 ha, embedded in mature forest (Fig. 1) (see Appendix A: Fig. 1). This range of sizes is common for the study region. The surveyed patches were spaced more than 1600 m apart. We used only patches at least 35 m in edge-to-edge distance from other open land uses such as arable fields. Almost all patches were surrounded by mature natural or plantation forests, which were unfavorable habitat patches for many bee species (Taki, Okochi et al., 2013). All of the young plantation patches were 4–6 years old. They had been created by cutting mature larch plantations, and the larches were replanted. Typically, young plantations are weeded until they are 3 years old in this region; therefore, the

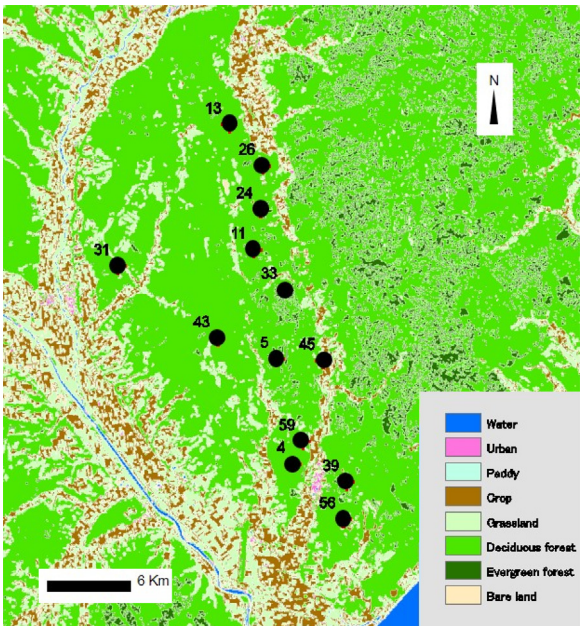


**Fig. 1.** Distribution of the 13 young plantation patches of *Larix leptolepis* in the study region (approximately 20 × 30 km, 42°54′N, 143°36′E) in the eastern Tokachi plain located in Urahoro and Ikeda, Hokkaido, Japan. The numbers are the Site IDs of the young plantation patches studied.

sampled patches were not weeded during the survey, except in parts of three patches. Within the three patches that had been partially weeded prior to the survey, we established plots only in the unweeded area (75–90% of patch area). A previous study reported that 314 plant species had been identified in the patches; frequently observed species included *Sasa nipponica, Carex* spp., *Rubus* spp., *Artemisia montana, Pachysandra terminalis, Eupatorium makinoi, Teucrium viscidum*, and *Petasites japonicas* (Yamaura, Connor, Royle, Itoh, Sato, Taki, et al., 2016).

## Bee sampling

We collected bees with 42-cm-diameter sweep-nets in the daytime (9:00–15:40) from 11 May to 25 June in 2011. A single collector visited each of the 13 young plantation patches five times, and covered the entire area of each in transects, walking the transects and sweeping the understory layers a variable number of times depending on the area of the patch, sweeping 100 times per ha, and walking 1 m per sweep (see Appendix A: Table 1). The bees collected in each of the five samples per patch were pooled. The surveys were conducted mainly on sunny days. We defined the sampling area with the use of net sweeping (1 m swept width was postulated) in each patch (1% of the patch area). In this way, we were able to account for sampling incompleteness (see next section). We chose not to use traps to collect bees, because traps can be disturbed by vertebrates in newly planted forest landscape areas (Saitoh & Nakatsu, 1997; Takatsuki, 2009). Voucher specimens were identified and deposited with the Forestry and Forest Products Research Institute, Tsukuba, Japan.

## Statistical analysis

We aggregated the number of collected individuals during the five visits, and treated the summed values as the number of individuals residing in the sampling plots. Although we acknowledge the existence of individuals not collected by our sweeping trials in the swept area (imperfect detection), our small sampling sizes did not allow us to consider imperfect detection and spatial incompleteness simultaneously. We followed the previously developed modeling frameworks (Yamaura, Connor, Royle, Itoh, Sato, Taki, et al. 2016; Yamaura, Kery, & Royle, 2016). Specifically, we assumed that expected number of individuals (abundance) of species $i$ in patch $j$ ($\lambda_{ij}$) was the function of patch area ($A_j$: ha):

$$\log(\lambda_{ij}) = \beta_{0i} + \beta_{1i} \times \log(A_j) \quad (1)$$

where $\beta_{0i}$ is logarithmically transformed expected abundance at $A_j = 1$. The slope coefficient $\beta_{1i}$ expresses the area dependence of the population density (Connor, Hosfield, Meeter, & Niu, 1997). When this value is larger than 1, density increases with area, and vice versa. When it does not deviate from 1, density remains constant with patch area.

'Realized' patch-level abundance ($z_{ij}$) was assumed to follow a Poisson distribution: $z_{ij} \sim \text{Poisson}(\lambda_{ij})$. We then modelled patch-level occupancy probability ($\psi_{ij}$), the probability that at least one individual occurs in the entire area of the patch, based on Eq. (1):

$$\psi_{ij} = 1 - \exp(-\lambda_{ij}). \quad (2)$$

We assumed that the number of collected individuals ($y_{ij}$) proportionally increases to the ratio of sampling area to patch area ($\phi_{ij}$):

$$y_{ij} \sim \text{Binomial}(z_{ij}, \phi_{ij}) \quad (3)$$

where it simply dictates that we expect that 1% of individuals would be collected when we sweep 1% of the studied patch.

We assumed that species-level parameters (e.g., $\beta_{0i}$) follow the normal distribution distancing mean and variations across species (community-level hyper-parameters): $\beta_{0i} \sim \text{Normal}\left(\mu_{\beta_0}, \sigma^2_{\beta_0}\right)$. We then obtained the community-

**Table 1.** Posterior distributions of community-level parameters.

| | Parameter | Mean | SD | 2.5% | 50% | 97.5% |
|---|---|---|---|---|---|---|
| (A) Model with DA and without random site effects | $\mu_{\beta 0}$ | −1.24 | 1.66 | −4.59 | −1.13 | 1.43 |
| | $\mu_{\beta 1}$ | 0.85 | 0.21 | 0.34 | 0.89 | 1.19 |
| | $\sigma_{\beta 0}$ | 2.64 | 0.76 | 1.36 | 2.60 | 4.26 |
| | $\sigma_{\beta 1}$ | 0.38 | 0.22 | 0.05 | 0.35 | 0.89 |
| | R | 117.50 | 52.45 | 49.00 | 106.00 | 226.00 |
| (B) Model without DA and with random site effects | $\mu_{\beta 0}$ | 1.01 | 0.52 | −0.07 | 1.04 | 1.91 |
| | $\mu_{\beta 1}$ | 1.06 | 0.26 | 0.57 | 1.06 | 1.57 |
| | $\sigma_{\beta 0}$ | 0.99 | 0.36 | 0.13 | 1.02 | 1.64 |
| | $\sigma_{\beta 1}$ | 0.38 | 0.24 | 0.01 | 0.36 | 0.85 |
| | $\mu_s$ | −0.23 | 0.41 | −0.98 | −0.26 | 0.67 |
| | $\sigma_s$ | 0.60 | 0.40 | 0.03 | 0.54 | 1.50 |

Posterior distributions of relevant parameters (mean values, SDs, and three percentiles) are shown. (A) The model considered missing species using the data augmentation (DA) technique. This model did not incorporate random site effects to capture variation not explained by patch area. Community-level parameters dictating mean ($\mu$) and standard deviation ($\sigma$) across species-level parameters are shown. R is an estimate of species pool size (regional species richness) that can occur within the studied habitat, which can have values ranging from 35 (number of collected species) to 235 (sum of collected and augmented species). (B) The model incorporated random site effects but did not consider missing species (did not use data augmentation and analyzed only collected species).

level estimates of species richness and total abundance at studied patches by enumerating the number of species with at least one individual ($\hat{z}_{ij} > 0$) and summed the predicted abundance ($\sum_{i=1} \hat{z}_{ij}$) across the species. We adopted a data augmentation technique to account for the existence of species that had not been recorded due to the partial coverage of our sweeping trials. Specifically, we augmented 200 potential species with zero collected individuals in any patch to the data matrix of the collected individuals (site × species matrix), which enabled us to infer the regional species richness of the studied habitat (R) and species richness and total abundance of individual patches by accounting for the uncollected species. We considered that 200 potential species, meaning that 235 species was the potential upper limit of the estimate, based on our knowledge about the species pool size. We finally constructed the SSR and AAR by obtaining species richness and total abundance with different patch areas of 0.01–9.90 ha as derived parameters, based on the prediction of species-level models.

We also fitted the model without data augmentation but with species-specific random site effects in Eq. (1) to quantify the variations in population densities unexplained by patch area: site.eff$_{ij} \sim$Normal $\left(0, \sigma^2_{s[i]}\right)$; $\log\left(1/\sigma^2_{s[i]}\right) \sim$Normal $\left(\mu_s, \sigma^2_s\right)$. We conducted this separate analysis because the sparseness of our data did now allow the simultaneous consideration of the missing species and random site effects in the single model. We estimated model parameters using Markov chain Monte Carlo (MCMC), and adopted conventional vague priors (e.g., $\mu_{\beta_0} \sim$Normal $\left[0, 100^2\right], \sigma_{\beta_0} =$ Uniform $[0, 5]$) for both models. Priors and model formulations were the same for two models except for the consideration of missing species and random site effects. We fitted the model with JAGS ver. 4.2.0 (Plummer, 2016), jagsUI ver. 1.4.2 (Kellner, 2016), and R ver. 3.3.1. (R Core Team, 2016). We discarded first 5000 iterations of three chains with different initial values, and ran

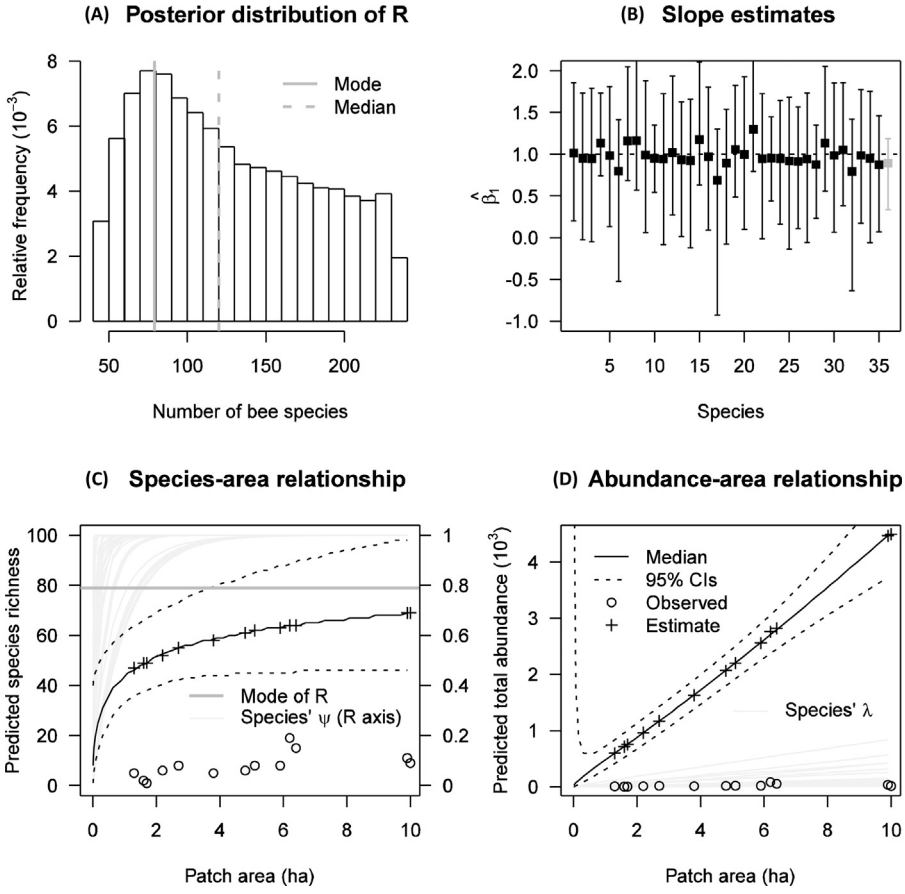


**Fig. 2.** Predictions derived from the hierarchical community model. (A) Estimates of species pool size (R), and their mode and median values are shown. Because this posterior distribution was obtained via independent Monte Carlo simulations, it is slightly different from that in Table 1. (B) Estimates of slope coefficients indicating the density responses of individual species to patch area. Median and 95% confidence intervals (CIs) are shown, where 1.0 indicates constant densities across the area. Species are numbered and aligned by their IDs (see Appendix A: Table 2 for species names). The rightmost estimate is the mean community value ($\mu_{\beta 1}$). (C, D) Inferred species richness/abundance–area relationships based on species-level models. Collected number of species/individuals per patch and their associated median estimates are also shown. Light gray lines represent the expected occupancy probability ($\Psi_{ij}$ on the right axis) and abundance ($\lambda_{ij}$) of individual species across the area.

additional sets of 100,000 iterations until convergence was achieved (assessed by 1.1 Gelman–Rubin statistic) with the function 'autojags' in jagsUI and parallel computing.

## Results

### Species pool size

We sampled 272 bee individuals by 30,745 sweepings, representing 35 species (5 Andrenidae, 8 Apidae, 3 Colletidae, and 19 Halictidae) from the 13 young plantation patches studied (see Appendix A: Table 2). We captured more than 10 individuals only for 8 species, which represented 65% of bee specimens. *Ceratine flavipes* was the most dominant species, comprising 21% of bee individuals bee individuals. Because our collected bee samples were small, the HCM yielded a wide confidential interval (CI) of species pool size: 79 mode estimate (Fig. 2A; Table 1).

### Model estimates and species/abundance–area relationships

We found no significant deviations from constant densities across patch areas at species and community levels (Fig. 2; Table 1). When we included random site effects into the species-level models, we found large among-site variation (median estimate of mean SD value across species $\bar{\sigma}_s = \left[1/\sqrt{\exp(\mu_s)}\right] = 1.14$) but still did not find deviations from the constant density hypothesis (see Appendix A: Fig. 2). These findings suggest that expected abundance ($\lambda_{ij}$) and occupancy probability ($\psi_{ij}$) of individual species and therefore community-level species richness and total abundance increased with patch area following the random placement model. Sampling (swept) area only partially covered the patch area, and the number of collected individuals increased with the number of sweeps. Estimated species richness and total abundance were much higher than the associated collected values (Fig. 2). Estimated species richness increased rapidly with the area in small areas (<2 ha), because the $\psi_{ij}$ values of most species increased within these areas (Fig. 2C). Total abundance was estimated to increase linearly with area (Fig. 2D). Total abundance had a relatively high upper limit within the 95% CIs at the lower limit of the range of area (= 0.01 ha).

## Discussion

We examined whether population densities of individual bee species changed with patch area. Although the use of net sweeping did not lead to the collection of large numbers of bees, this method enabled us to specify the sampling area (and therefore unsampled area). Additionally, the HCM yielded SARs and AARs by accounting for the incomplete spatial coverage of the field sampling. Modeling work showed that the population densities of individual species remained unchanged with area; that is, the per area conservation value of early-successional stages of larch plantations was similar irrespective of area. As the random placement model postulates, bee species richness and total abundance were predicted to increase with area. Estimated species richness increased rapidly with area in small areas (< 2 ha) because occupancy probabilities of most species increased within these areas. This suggests that a large young plantation patch could harbor species richness and total abundance comparable to those of small patches (see Appendix A: Fig. 3). Although large habitat patches are widely accepted to have conservation value, our results imply the value of small habitat patches in fragmented landscapes, which is consistent with previous studies (Baldi, 2008; Fischer & Lindenmayer, 2002; Tscharntke, Steffan-Dewenter, Kruess, & Thies, 2002).

There are some limitations to our study. We tested patch sizes ranging from 1.3 to 10 ha, which were representative sizes for forest logging and planting in the study region. The trend in SAR for much larger areas (> 10 ha) remains unclear. The contribution of much smaller patches (< 1.3 ha) is also uncertain. Experimental evidence has shown that small grassland-like patches (< 1 ha) had different community compositions from large patches and rare species were mostly confined to large patches in the case of European plants and herbivorous animals (Rösch, Tscharntke, Scherber & Batáry, 2015). Additionally, our bee samples were small, and in turn the estimate of species pool size was diffusive. We recorded 35 bee species based on a small sample of individuals; therefore, the model yielded 79 mode and over 100 median estimates of species pool size (regional species richness) and the confidence interval was quite large. When we used 100 (rather than 200) as the number of augmented species, the mode and median estimates changed into 60 and 87, respectively. Although the mode estimates were relatively robust, the estimation could not be conclusive. We also made the assumption that bee densities did not change within patches though we surveyed the homogeneously managed plantation habitats. We conducted sampling over a period of 2 months (five times per patch); this sampling effort may not have fully covered the seasonal occurrence of bees. Early successional forest shows a higher temporal turnover in bee species richness compared with that in old-growth forest (Rodríguez & Kouki, 2016). Furthermore, we sampled bees by net sweeping to standardize the sampled area to 1% of area in each patch, which may lead that smaller spatial sampling coverage implies shorter sampling time of sweep netting on plants. This might underestimate abundances and species richness of bees in smaller patches.

Large random site effects shown in the analyses may suggest that focusing on environmental factors other than patch area would significantly improve the conservation returns of early-successional plantations. Candidate factors include plantation age, patch shape, topography, and plant composition. For example, during the field survey, some patches

had many flowering plants (e.g., *Stellaria* spp.) with visiting bees, whereas some were predominately covered by dwarf bamboo, *Sasa nipponica*. Valuing small patches and acknowledging factors other than patch area would broaden conservation options and make conservation practices more feasible (Huth & Possingham, 2011).

This study was conducted in Japan, where the area of young forests and semi-natural grasslands has declined rapidly (Yamaura et al., 2012), although about 70% of Japan is covered by forest, of which over 40% is plantation (MAFF, 2015). Consequently, a national decline in animals, such as bird and butterfly species that are dependent on early successional forests, has also been reported (Inoue, 2005; Yamaura et al., 2009). In Japan, forestry activities such as logging and planting have declined since the 1960s with the increase in imported timber, although the wood supply from the forests has increased slightly (Yamaura et al., 2012) as public demand for domestic timber has increased. Our results support the use of Japanese tree plantations to generate early-successional forests to contribute to wild bee conservation and restoration.

Active forest management options can contribute to maintaining regional diversity in some pollinator groups. For example, 81% of the total regional species pool of butterflies in Estonia is found in forest clear-cuts, suggesting that managed forests substantially mitigate the loss of butterfly diversity elsewhere (Viljur & Teder 2016). In the future, it will be necessary to test how other forest management options influence our findings. Previous studies showed that tree thinning positively affected bee and other pollinator diversity (Taki et al., 2010) and the frequent clearing and removal of woody debris increased bee diversity after logging and power line clearing (Sydenham, Moe, Stanescu-Yadav, Totland, & Eldegard 2016). Finding such effective forest management options at both local and landscape scales for early successional forest should contribute to maintaining and improving the habitat for bee species and other pollinators.

When planning the extent and location of forest cutting and replanting, some needs should be considered. There could be vulnerable species with small populations or specialist species of wild bees inhabiting mature and old-growth forests (Taki, Makihara et al., 2013). Furthermore, trade-offs in ecosystem services should also be considered carefully in the plans (Bennett, Peterson, & Gordon 2009; Chan, Shaw, Cameron, Underwood, & Daily 2006). These trade-offs can be between bee diversity and other taxonomic diversity or between pollination and other ecosystem services, such as timber production, carbon storage, water provision, and flood control, which are provided by mature forests. Nevertheless, our results are consistent with a positive SAR for bees in early-successional planted forests, at least within the tested range of areas. These findings in relation to management operations for forests and plantations suggest that small patches of early successional forest contribute to conserve and restore wild bee diversity.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2017.09.002.

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