Succession Influences Wild Bees in a Temperate Forest Landscape: The Value of Early Successional Stages in Naturally Regenerated and Planted Forests

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Abstract

In many temperate terrestrial forest ecosystems, both natural and human disturbances drive the reestablishment of forests. Succession in plant communities, in addition to reforestation following the creation of open sites through harvesting or natural disturbances, can affect forest faunal assemblages. Wild bees perform an important ecosystem function in human-altered and natural or seminatural ecosystems, as they are essential pollinators for both crops and wild flowering plants. To maintain high abundance and species richness for pollination services, it is important to conserve and create seminatural and natural land cover with optimal successional stages for wild bees. We examined the effects of forest succession on wild bees. In particular, we evaluated the importance of early successional stages for bees, which has been suspected but not previously demonstrated. A range of successional stages, between 1 and 178 years old, were examined in naturally regenerated and planted forests. In total, 4465 wild bee individuals, representing 113 species, were captured. Results for total bees, solitary bees, and cleptoparasitic bees in both naturally regenerated and planted conifer forests indicated a higher abundance and species richness in the early successional stages. However, higher abundance and species richness of social bees in naturally regenerated forest were observed as the successional stages progressed, whereas the abundance of social bees in conifer planted forest showed a concave-shaped relationship when plotted. The results suggest that early successional stages of both naturally regenerated and conifer planted forest maintain a high abundance and species richness of solitary bees and their cleptoparasitic bees, although social bees respond differently in the early successional stages. This may imply that, in some cases, active forest stand management policies, such as the clear-cutting of planted forests for timber production, would create early successional habitats, leading to significant positive effects for bees in general.

Citation: Taki H, Okochi I, Okabe K, Inoue T, Goto H, et al. (2013) Succession Influences Wild Bees in a Temperate Forest Landscape: The Value of Early Successional Stages in Naturally Regenerated and Planted Forests. PLoS ONE 8(2): e56678. doi:10.1371/journal.pone.0056678

Editor: Jeff Ollerton, University of Northampton, United Kingdom

Received July 17, 2012; Accepted January 16, 2013; Published February 15, 2013

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Funding: This study was funded as a project of the Research Institute for Humanity and Nature and was also supported in part by the Global Environment Research Fund (S-9) of the Ministry of the Environment, Japan. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

In many temperate terrestrial forest ecosystems, natural disturbances such as avalanches, windstorms, fires, and floods, and human disturbance including tree harvesting, drive the reestablishment of forests [1]. Succession in plant communities, in addition to reforestation following the creation of open sites through harvesting or natural disturbances, can affect forest faunal assemblages. For example, the intermediate disturbance hypothesis suggests that shifts in species richness are likely and the midway stage of succession would contain the highest species richness [2,3]. Previous studies have consistently demonstrated that the species richness of various taxa peak at different times as succession proceeds, indicating that the diverse taxa within a community include species that prefer specific successional stages [4,5]. Among the wide range of forest successional stages, the conservational and ecological importance and the value of the early stages of succession may require more attention [6]. The early successional stage can be characterized by high productivity of plants, compound floral and faunal food webs, and large nutrient changes [6]. Previous studies have shown that this stage in a temperate forest region can have a great diversity in abundance and species richness of flora and fauna [7,8].

Wild bees perform an important ecosystem function in human-altered and natural or seminatural ecosystems as bee species are important pollinators for both crops and wild flowering plants [9]. Pollinators including wild bees can increase the production of approximately 75% of the 115 most essential crops worldwide [10], and the proportion of flowering plants pollinated by animals is estimated to be 87.5% of all flowering plants [11]. The conservation and creation of seminatural and natural land cover at optimal successional stages for wild bees are important to maintain a high abundance and species richness for pollination services [12,13]. Examples of this include human-dominated landscapes
with a long history of human land use, among which grasslands are a notable seminatural habitat. One study on wild bees, covering a period of 1 to 5 years of secondary succession of European fallow land, found the highest species richness after 2 years [14]. However, another study of wild bees in European limestone quarries found little difference in abundance and species richness among habitats ranging from 1 to 121 years old [15].

Figure 1. The study region in the northern part of Ibaraki Prefecture in central Japan (approximately 36°50′–7′ N, 140°32′–8′ E; 500–500 m above sea level) and locations of the study stands within areas of planted conifers and naturally regenerated forests. Numbers indicate reforestation age.

doi:10.1371/journal.pone.0056678.g001

Table 1. Study sites, 10 naturally regenerated and 8 conifer (Cryptomeria japonica) planted forest stands, in the northern part of Ibaraki Prefecture in central Japan (approximately 36°50′–57′ N, 140°32′–38′ E; 500–850 m above sea level).

| ID | Reforestation type | Age | Area (ha) |
|----|--------------------|-----|-----------|
| N1 | Natural            | 1   | 2.53      |
| N4 | Natural            | 4   | 4.91      |
| N12| Natural            | 12  | 4.13      |
| N24| Natural            | 24  | 23.56     |
| N51| Natural            | 51  | 10.37     |
| N54| Natural            | 54  | 14.72     |
| N71| Natural            | 71  | 19.11     |
| N128| Natural        | 128 | 32.49     |
| N174| Natural        | 174 | 11.75     |
| N178| Natural        | 178 | 9.29      |
| C3 | Conifer planted   | 3   | 4.28      |
| C7 | Conifer planted   | 7   | 6.04      |
| C9 | Conifer planted   | 9   | 4.9       |

Table 1. Cont.

| ID | Reforestation type | Age | Area (ha) |
|----|--------------------|-----|-----------|
| C20| Conifer planted    | 20  | 4.88      |
| C29| Conifer planted    | 29  | 14.29     |
| C31| Conifer planted    | 31  | 12.07     |
| C75| Conifer planted    | 75  | 3.13      |
| C76| Conifer planted    | 76  | 2.55      |
| Mean|                   |     | 52.61 10.28 |

Stand ages were based on tentative estimations recorded in the National Forest Inventory of Japan.

doi:10.1371/journal.pone.0056678.t001
Successional Influences on Bees

A. Abundance, all

\[ y = -217.8 \ln(x) + 927.59 \quad R^2 = 0.4764 \]

\[ y = -96.18 \ln(x) + 515.51 \quad R^2 = 0.3006 \]

B. Species richness, all

\[ y = -6.342 \ln(x) + 55.434 \quad R^2 = 0.6134 \]

\[ y = -16.3 \ln(x) + 75.894 \quad R^2 = 0.7432 \]

C. Abundance, social

\[ y = 0.0354x^2 - 2.913x + 60.546 \quad R^2 = 0.3993 \]

\[ y = 0.1261x + 10.611 \quad R^2 = 0.4907 \]

D. Species richness, social

\[ y = 0.2924 \ln(x) + 2.3935 \quad R^2 = 0.5097 \]

E. Abundance, solitary

\[ y = -178.8 \ln(x) + 742.12 \quad R^2 = 0.5148 \]

\[ y = -87.64 \ln(x) + 476.02 \quad R^2 = 0.2956 \]

F. Species richness, solitary

\[ y = -4.646 \ln(x) + 40.195 \quad R^2 = 0.5902 \]

\[ y = -13 \ln(x) + 58.252 \quad R^2 = 0.7817 \]

G. Abundance, cleptoparasitic

\[ y = -34.03 \ln(x) + 140.39 \quad R^2 = 0.437 \]

\[ y = -12.37 \ln(x) + 69.282 \quad R^2 = 0.6569 \]

H. Species richness, cleptoparasitic

\[ y = -1.989 \ln(x) + 12.846 \quad R^2 = 0.6916 \]

\[ y = -3.241 \ln(x) + 14.348 \quad R^2 = 0.6053 \]
indicates that even newly created and permanent grassland-like habitats provide important habitats for wild bees.

In regions dominated by temperate forests, bee abundance and species richness within the forest area are known to increase with decreasing forest cover in the surrounding landscape [16]. This finding suggests that even if an optimal habitat for bees were created, a rapid decrease in abundance and species richness would occur with habitat succession in regions where forest regeneration to canopy closure occurs rapidly from grassland-like habitats. Rapid forest regeneration to canopy closure of matured and old-growth forest provides a habitat for closed-forest wildlife but presents a trade-off with early successional species [6,8]. Therefore, optimal management of the successional stages of seminatural habitat would help to maintain high abundance and species richness of bees at regional and landscape scales, providing effective pollination services.

We aimed to determine the optimal successional stages, and to propose better management practices of seminatural habitat, for wild bees in a temperate forest region, in order to ensure pollination services in the region. We examined the effects of reforestation stages, from recently harvested to old growth forests between 1 and 178 years old. Bee assemblages were examined for the two different reforestation types of planted conifer and naturally regenerated forests. Plant species composition regularly varies between different types and ages of reforestation [17]. Here, we tested the hypothesis that the different successional stages of seminatural habitats would affect the abundance and species richness of wild bees, but the responses of wild bees might differ depending on the characteristics of the bees (i.e., social or parasitic status). We particularly assessed the importance of the early successional stages for bees, which has been suspected but not previously proven [18]. We conducted this study in Japan, where the most intensive anthropogenic reforestation efforts involve the conversion of natural or seminatural broad-leaved forests to monocultures of conifer trees. To accommodate the high demand for timber after the Second World War, broad-leaved trees were harvested and coniferous species, primarily Cryptomeria japonica, Chamaecyparis obtusa, and Larix leptolepis, were planted until the 1970s. Such conifer plantations now account for approximately 40% of the total forest cover in Japan [19].

Materials and Methods

Study Region and Sites

The study region was the northern part of Ibaraki Prefecture in central Japan (approximately 36°50′–7°N, 140°32′–8°E; 500–50 m above sea level). The annual mean temperature of the study region is 10.7°C, and the mean annual precipitation is 1910 mm [20]. The landscapes have undergone dramatic anthropogenic changes since the Second World War. Intensive planted reforestation conducted in this area has converted the landscape from natural or seminatural forests of broad-leaved trees, dominated by Quercus serrata, Quercus mongolica, and Fagus crenata to monoculture conifer plantations of Cryptomeria japonica and Chamaecyparis obtusa [21]. For this study, 10 naturally regenerated deciduous forest stands (2.53–32.49 ha) and eight planted conifer (C. japonica) forest stands (2.53–14.29 ha) were selected (Table 1; Figure 1). The ages of the naturally regenerated forest stands varied between 1 and 178 (1, 4, 12, 24, 51, 54, 71, 128, 174, and 178) years old after harvest. The ages of planted forest stands varied between 3 and 76 (3, 7, 9, 20, 29, 31, 75, and 76) years old after harvest. The conifer plantation trees in the study region are usually harvested at around 80 to 90 years of age. The ages were based on a tentative estimation of the National Forest of Japan.

Bee Collection

We collected wild bees using standard Townes-type Malaise traps (Golden Owl Publishers; 180 cm long, 120 cm wide, and 200 cm high) [22] in 2002 for naturally regenerated forests and 2003 for planted conifer forests. In each of the selected forest stands, two traps were placed approximately in the center of the forest stand to avoid forest edge effects. A mixture of ethanol and propylene glycol was used to preserve bees captured in the Malaise traps. Trapped wild bees were collected every 2 weeks from late April to early November in both forest types. We brought all collected bees into the laboratory at the Forestry and Forest Products Research Institute, Tsukuba, where voucher specimens were kept, and identified at the species level. We then classified cleptoparasitic Coelioxys, Epeolus, Nomada, and Sphexidae species as “cleptoparasitic,” social Apis and Bombus species as “social,” and the remaining species as “solitary.” Although there may have been some species of primitively eusocial bees in the “solitary” group, such as species in the family Halictidae [23], we tentatively classified them as solitary because of the limited available information on their biology.

Data Analysis

The effects of the successional stage of reforestation for both forest types on the abundance and species richness of bee groups (all, social, solitary, and cleptoparasitic bee assemblages) were determined using ordinary least-squares regression models. We conducted simple and quadratic functions because scatterplots used previously indicated that some results might have nonlinear effects from the successional stages. We disqualified results from the quadratic functions when the vertexes placed within the forest ages (between 3 and 76 years old for planted forest and between 1 and 178 years old for naturally regenerated forest) indicated values below 0 on the y axis, which were biologically illogical situations because bee abundance and species richness became minus values. As well as the simple linear and quadratic regression models, we examined models in which the successional stages of reforestation were square-root and log transformed. We then compared the models using Akaike’s information criterion (AIC), the ΔAIC values obtained by the difference from AIC values of the null model. All of the analyses were performed using the R software (version 2.15.0) [24]. Prior to these regression analyses, we used Mantel tests to check for significant spatial autocorrelation among the study sites for the abundance and species richness of bees in naturally regenerated and planted conifer forest stands; no autocorrelation was found (all p>0.400). The ade4 package of R, with the number of permutations set to 1000, was used for the Mantel tests [25].
Table 2. Model comparisons, for the abundance and species richness of bee groups (all, social bees, solitary bees, and cleptoparasitic assemblages) in natural regenerated forest.

| All bees | Social | Solitary | Cleptoparasitic |
|----------|--------|----------|-----------------|
|          | AIC    | ΔAIC     | AIC             | AIC             | ΔAIC     | AIC     | ΔAIC |
|          | abundance | species richness | abundance | species richness | abundance | species richness | abundance | species richness |
| null     | 145.369 | 83.856   | 24.169          | 81.285          | 2.211    | 76.538  | 59.459 |
| y = x    | 145.765 | 0.396    | 2.211           | 76.538          |         |         |      |
| y = x²   | 145.451 | 0.082    | 1.474           | 79.816          |         |         |      |
| y = log(x)| 143.794 | 1.575    | 7.504           | 78.338          |         |         |      |
| y = sqrt(x)| 144.667 | 2.312    | 8.698           | 77.671          |         |         |      |

The table shows values of AIC and of ΔAIC calculated as the difference from AIC values of the null models.

Discussion

The response of all bees to the different successional stages indicated that the naturally regenerated and planted forest sites were equally valuable to bee community structure and diversity. The abundance and species richness of all bees were highest in the early successional stage of planted forest, followed by naturally regenerated forests. This result is consistent with previous studies that show that early successional stages provide important habitats for bees. The abundance and species richness of all bees were higher in planted forests than in naturally regenerated forests, which may be due to the differences in habitat availability and quality. For example, planted forests are often managed with clear-cutting and thinning, which create more open and early successional habitats. In contrast, naturally regenerated forests may have more closed canopies and less disturbance, which may explain the lower abundance and species richness observed in these forests.

Social bees were the most abundant group in all successional stages, with the highest abundance and species richness observed in the early successional stages of planted forests. This result suggests that social bees are well adapted to early successional habitats. Solitary bees were more abundant in the mid-successional stages, where they may find nectar sources and nesting sites. Cleptoparasitic bees were the least abundant group, with the highest abundance and species richness observed in the late successional stages of planted forests. This result is consistent with previous studies that show that cleptoparasitic bees are more common in later successional stages, where they may find host species that they parasitize.

Results

We captured and identified a total of 445 wild bee individuals from 13 species, 4 social (Bombus hypocrita, Bombus ardens, Bombus pensylvanicus, Bombus rufocinctus) and 10 solitary (Ceratina, Coelioxys, Halictus, Lasioglossum, Melissodes, Andrena, Nomada, Osmia, Sphecodes, Xylocopa) species. Model comparisons for the naturally regenerated forest indicated that the simple linear regression model was selected for the abundance of social bees, and the log-transformed regression model was selected for the species richness of social bees. Model comparisons for the planted forest indicated that the simple linear regression model was selected for the abundance of all bees, and the log-transformed regression model was selected for the species richness of all bees. Model comparisons for the other categories (Table 2) indicated that the simple linear regression model was selected for the abundance of social bees, and the log-transformed regression model was selected for the species richness of social bees.

For example, in Japan, the area of grassland and young forests has declined rapidly to the extent that 68% of the national land area is covered by forest. This change has been due to the increased demand for forest products and the increased attention to environmental conservation. The increased forest cover has also led to increased habitat availability for bees, which may explain the increased abundance and species richness observed in planted forests.

Conclusions

Our results demonstrate the importance of considering the successional stage of forests when studying bee communities. The abundance and species richness of bees are highest in early successional stages, which may provide important habitats for bees. The differences in abundance and species richness observed between naturally regenerated and planted forests indicate the need for conservation efforts to maintain and restore early successional stages in forests.

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system [31]. Many of the trees in planted forests are now reaching harvest age, although the wood supply from the forests has slightly increased [29]. As the area of grassland and early successional forests in Japan has declined, a national decline in bird and butterflies species, which are dependent on early successional stages, is also thought to have occurred [32,33]. Trade-offs must be carefully considered when planning the extent and location of forest cutting. These trade-offs can be between bee diversity and other taxonomic diversity, or between pollination and other ecosystem services [34], such as carbon storage, flood control, water provision, and timber production, which are provided by mature naturally regenerated and planted forests. Some active clear-cutting of planted forests, leading to early succession, might become an acceptable policy in Japan, although conservation of primary, old growth natural forests and careful rotation planning of where to cut, at both a landscape and national scale, are required.

Wild bees pollinate various crops [35–40]. The area surrounding bee-pollinated crop fields would ideally be a grassland-like habitat, and hence the management and quality maintenance of seminatural and natural ecosystems around agricultural fields are important [41,42]. For the example of almond production in California, it was found that practices within farms, such as organic farming alone, would not sustain pollination services by wild bees, and the presence of high-quality habitats along the edges of the orchards are important [43]. In many temperate terrestrial forest ecosystems, forest regeneration to canopy closure occurs quickly; hence the creation and maintenance of early successional stages of both naturally regenerated and planted conifer forests, surrounding bee-pollinated crop land could help to enhance pollination services. For example, near the present study region, in the northern part of Ibaraki Prefecture in central Japan, common buckwheat, which is a heterostylous crop that depends highly on insect pollination, is a distinctive crop grown by local landholders in mountainous regions [39,44]. Such a crop might benefit from the habitats created for bees.

Although the species richness of the social bees collected was relatively low (four species), our results indicated that the responses of social bee species to the different forest successional stages were different from those of solitary and cleptoparasitic bees. As the successional stages progressed, positive relationships were observed for the abundance and species richness of social bees in naturally regenerated forest. However, as successional stages progressed, the convex relationship for abundance and no relationship for the species richness of social bees were observed in planted conifer forest. In naturally regenerated forest, nesting resources might be more widely available in mature successional stages than in early successional stages. This could include cavities in large trees for Apis cerana [43,46] and underground cavities for the Bombus species [47]. In planted conifer forests, the early successional stages may provide floral resources for the Apis and Bombus bees; on the other hand, late successional stages (e.g., the 75- and 76-year-old stands) may have lower floral resources but more underground cavities for nesting sites for Bombus species. Planted forests are usually disturbed by active human management, such as pre-commercial tree thinning and understory weed clearing [40]; thus the 20- and 31-year-old forest stands might have contained fewer nesting sites for the Bombus species as well as poorer floral resources. It is important to interpret our results considering the effects of wider spatial scales on Apis and Bombus species [49]. The foraging ranges of these social bees are likely wider than those of the majority of the solitary bees [50–52]. Previous studies have indicated that Apis cerana forages over 1 km [53] and the spatial ranges of landscape effects, which influenced its foraging, were from 1 to 3 km [39,41]. Although the foraging ranges of our captured Bombus species were unknown, other Bombus species have been known to forage for at least 250 m to 1.5 km [34–37]. Therefore, influences at the landscape level rather than at the forest stand level might have influenced these responses of these social bees.

Wild bees were sampled during a single year in each reforestation type using Malaise traps in the present study. There was a risk that this particular sampling method may be biased for or against particular groups of bees, and may not represent sampling completeness of the bee fauna in the study region. However, we sampled 4463 wild bee individuals from 113 species using the Malaise traps. Based on the sampled bees, we can conclude that the early successional stages of both naturally regenerated and planted conifer forests maintain high abundances and species richness of solitary bees and their cleptoparasitic bees, although social bees respond differently in early successional stages. These results may have implications for active forest stand management practices, such as clear-cutting of planted forests for timber production, which would create early successional habitats, leading to significant positive effects on bees in general. However, in addition to the conservation of primary, old growth natural forests, trade-offs between bee diversity and other taxonomic diversity in relation to pollination and other ecosystem services should be considered.

### Table 3. Model comparisons for the abundance and species richness of bee groups (all, social bees, solitary bees, and cleptoparasitic assemblages) in conifer (Cryptomeria japonica) planted forest.

| Model | AIC | ΔAIC | AIC | ΔAIC | AIC | ΔAIC | AIC | ΔAIC | AIC | ΔAIC |
|-------|-----|------|-----|------|-----|------|-----|------|-----|------|
| null  | 119.883 | 74.847 | 79.729 | 18.516 | 116.102 | 70.825 | 90.871 | 50.644 |
| y = x  | 118.666 | 1.216 | 72.215 | 2.631 | 81.719 | 1.989 | 20.146 | 1.630 | 114.341 | 1.761 | 67.709 | 3.115 | 89.577 | 1.294 | 48.900 | 1.743 |
| y = x² | 115.345 | 3.626 | 58.358 | 11.309 | 79.653 | 0.077 | 18.751 | 0.235 | 110.824 | 5.278 | 51.292 | 19.533 | 88.165 | 2.706 | 42.407 | 2.326 |
| y = log(x) | 116.706 | 3.176 | 65.972 | 8.875 | 81.418 | 1.689 | 20.431 | 1.915 | 112.316 | 3.786 | 60.649 | 10.176 | 88.276 | 2.595 | 45.207 | 5.437 |
| y = sqrt(x) | 117.410 | 2.472 | 69.494 | 5.353 | 81.683 | 1.953 | 20.463 | 1.947 | 112.973 | 3.129 | 64.698 | 6.126 | 88.590 | 2.281 | 47.018 | 3.626 |

The table shows values of AIC and of ΔAIC calculated as the difference from AIC values of the null models. Asterisks (*) indicate that the vertexes placed within the forest ages (between 3 and 76 years old for planted conifer forest) were below 0 on the y axis for the best models (quadratic functions), and thus the second-best models were selected.

doi:10.1371/journal.pone.0056678.t003
Supporting Information

Table S1 List of bee species and the number of individuals sampled in each forest stand.

Author Contributions
Conceived and designed the experiments: HT KO TI SM. Performed the experiments: HT KO TI HG TM SM. Analyzed the data: HT SM. Wrote the paper: HT SM.

Acknowledgments
We thank T. Kitajima and K. Meshiai for the care of bee samples in the laboratory.

References
1. Oliver CD, Larson BC (1996) Forest Stand Dynamics, Updated Edition. New York: Wiley. 320 p.
2. Grime JP (1973) Competitive exclusion in herbaceous vegetation. Nature 242: 331–334.
3. Connell JH (1973) Diversity in tropical rain forests and coral reefs - High diversity of trees and corals is maintained only in a nonequilibrium state. Science 199: 1302–1310.
4. Pickert STA, Thompson JN (1978) Patch dynamics and the design of nature reserves. Biological Conservation 13: 27–37.
5. Spies TA, Turner MG (1999) Dynamic forest mosaics. In: Hunter ML, editor. Maintaining biodiversity in forest ecosystems. Cambridge: Cambridge University Press. pp. 95–160.
6. Swanson ME, Franklin JF, Beschta RL, Grissell CM, DellaSala DA, et al. (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9: 117–125.
7. Fontaine JB, DeoVC, Brusven WB, Law KE, Kaufman JB (2009) Bird communities following high-severity fire: Response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. Forest Ecology and Management 257: 1496–1504.
8. Yamaura Y, Royle JA, Shinada N, Asanuma S, Sato T, et al. (2012) Biodiversity of man-made open habitats in an underused country: a class of multispecies abundance models for count data. Biodiversity and Conservation 21: 1365–1380.
9. Corbet SA, Williams IH, Osborne JL (1991) Bees and the pollination of crops and wild flowers in the European community. Bee World 72: 47–59.
10. Klein AM, Vaisiere BE, Cané JH, Steffan-Dewenter I, Cunningham SA, et al. (2007) Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society of London B 274: 303–313.
11. Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120: 321–326.
12. Kremen C, Williams NM, Bugg RL, Fay JP, Thorp RW (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecology Letters 7: 1109–1119.
13. Winfree R (2010) The conservation and restoration of wild bees. In: Ostfeld RS, Schleisinger WH, editors. Year in Ecology and Conservation Biology 2010. Malden: Wiley-Blackwell. pp. 169–197.
14. Steffan-Dewenter I, Tscharntke T (2001) Succession of bee communities on fallows. Ecology 82: 83–93.
15. Kraus J, Alpert T, Steffan-Dewenter I (2009) Habitat area but not habitat age determines wild bee richness in limestone quarries. Journal of Applied Ecology 46: 194–202.
16. Winfree R, Griswold T, Kremen C (2007) Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology 21: 213–225.
17. Fujimori T (2001) Ecological and silvicultural strategies for sustainable forest management. Amsterdam: Elsevier.
18. Winfree R, Baronoukis I, Cariveau DP (2011) Native pollinators in anthropogenic habitats. Annual Review of Ecology, Evolution, and Systematics 42: 1–22.
19. Statistics-Department (2008) The 62nd Statistical Yearbook of Ministry of Agriculture Forestry and Fisheries, Japan 2006–2007. Tokyo: Statistics Department, Ministry of Agriculture Forestry and Fisheries, Japan.
20. Mizoguchi Y, Morisawa T, Ohtani Y (2002) Climate of Ogasawara forest reserve. In: Nakashizuka T, Matsumoto Y, editors. Diversity and interaction in a temperate forest community. Ogasawara forest reserve of Japan. Tokyo: Springer. pp. 11–18.
21. Makino S, Goto H, Hasegawa M, Okabe K, Tanaka H, et al. (2007) Degradation of longicorn beetle (Coleoptera, Cerambycidae, Disteniidae) fauna caused by forest clear-cutting to man-made forest stands of Cryptomeria japonica (Taxodiaceae) in central Japan. Ecological Research 22: 372–381.
22. Makino S, Goto H, Inoue T, Sueyoshi M, Okabe K, et al. (2006) The monitoring of insects to maintain biodiversity in Ogasawara forest reserve. Environmental Monitoring and Assessment 120: 477–485.
23. Michener CD (2007) The bees of the world. Baltimore: The Johns Hopkins University Press.
24. Development Core Team (2012) R, a language and environment for statistical computing. Vienna: R Foundation for statistical computing.
25. Dray S, Dufour AB (2007) The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22: 1–20.
26. Taki H, Keven PG, Ascher JS (2007) Landscape effects of forest loss in a pollination system. Landscape Ecology 22: 1537–1537.
27. Taki H, Keven PG, Ascher JS (1992) Strategy for conservation of wild bees in an agricultural landscape. Agriculture Ecosystems & Environment 40: 179–192.
28. Osborne JL, Williams IH, Corbet SA (1991) Bees, pollination and habitat change in the European Community. Bee World 72: 99–116.
29. Yamaura Y, Oka H, Taki H, Ozaki K, Tanaka H (2013) Sustainable management of planted landscapes: lessons from Japan. Biodiversity and Conservation 21: 3107–3129.
30. FAO (2007) State of the world’s forests 2007. Rome: Food and Agriculture Organization of the United Nations.
31. Nagy A (1988) International trade in forest products; Nagy A, editor. Bicester: AB Academic Publishers.
32. Yamaura Y, Ikeno S, Sano M, Okabe K, Ozaki K (2009) Bird responses to broad-leaved forest patch area in a plantation landscape across seasons. Biological Conservation 142: 2155–2163.
33. Inoue T (2005) Causes of butterfly decline in Japan. Japanese Journal of Entomology (New Series) 8: 43–64.
34. Chan KMA, Shaw MR, Cameron DR, Underwood EC, Daily GC (2006) Matrix quality determines pollinator abundance in crop fields. Ecology Letters 9: 1103–1113.
35. Basset M, van der Sluis G, Violle C, Thuiller W (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee losses. Ecology Letters 14: 1062–1072.
36. Klein AM, Brittain C, Hendrix SD, Thorp R, Williams N, et al. (2012) Wild pollination services to California almond rely on semi-natural habitat. Journal of Applied Ecology 49: 723–732.
37. Taki H, Okabe K, Yamaura Y, Matsuzaki T, Sueyoshi M, et al. (2010) Effects of landscape metrics on Apis and non-Apis pollinators and seed set in common buckwheat. Basic and Applied Ecology 11: 594–602.
38. Klein AM, Steffan-Dewenter I, Tscharntke T (2003) Bee pollination and fruit set of Coffea arabica and C.canephora (Rubiaceae). American Journal of Botany 90: 153–157.
39. Taki H, Yamaura Y, Okabe K, Maeto K (2011) Plantation vs. natural forest: Matrix quality determines pollinator abundance in crop fields. Scientific Reports 1: 1–13.
40. Garibaldi LA, Steffan-Dewenter I, Kremen C, Morales JM, Bommarco R, et al. (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee losses. Ecology Letters 14: 1062–1072.
41. Klein AM, Brittain C, Hendrix SD, Thorp R, Williams N, et al. (2012) Wild pollination services to California almond rely on semi-natural habitat. Journal of Applied Ecology 49: 723–732.
42. Taki H, Okabe K, Makino S, Yamaura Y, Sueyoshi M (2009) Contribution of small insects to pollination of common buckwheat, a distylous crop. Annals of Applied Biology 155: 121–129.
43. Saeki M (1999) Wonders of the Japanese honeybee - Biological of Northernmost Apis cerana - . Tokyo: Kaiyuisha.
44. Yoshida T (2000) Rearing method and ecology of Japanese honeybee. Tokyo: Tamagawa University Press.
45. Sakagami S, Katayama E (1977) Nests of some Japanese bumblebees (Hymenoptera, Apidae). Journal of the Faculty of Science, Hokkaido University Series VI Zoology 21: 92–153.
46. Hirota A, Sakai T, Takahashi K, Sato T, Tanouchi H, et al. (2011) Effects of management, environment and landscape conditions on establishment of hardwood seedlings and saplings in central Japanese coniferous plantations. Forest Ecology and Management 262: 1280–1288.
47. Steffan-Dewenter I, Münzberg U, Burger C, Thies C, Tscharntke T (2002) Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83: 1421–1432.
48. Gathmann A, Tscharntke T (2002) Foraging ranges of solitary bees. Journal of Applied Ecology 39: 705–717.
49. Zurbrüchner A, Landert L, Klaiber J, Muller A, Hein S, et al. (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation 143: 660–676.
52. Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153: 589–596.
53. Dyer FC, Seeley TD (1991) Dance dialects and foraging range in three Asian honey bee species. Behavioral Ecology and Sociobiology 28: 227–233.
54. Knight ME, Martin AP, Bishop S, Osborne JL, Hale RJ, et al. (2005) An interspecific comparison of foraging range and nest density of four bumblebee (Bombus) species. Molecular Ecology 14: 1811–1820.
55. Osborne JL, Clark SJ, Morris RJ, Williams IH, Riley JR, et al. (1999) A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. Journal of Applied Ecology 36: 519–533.
56. Osborne JL, Martin AP, Carreck NL, Swain JL, Knight ME, et al. (2008) Bumblebee flight distances in relation to the forage landscape. Journal of Animal Ecology 77: 406–415.
57. Wolf S, Moritz RFA (2008) Foraging distance in Bombus terrestris L. (Hymenoptera: Apidae). Apidologie 39: 419–427.