RESEARCH Open Access



Effects of vegetation structure and human impact on understory honey plant richness: implications for pollinator visitation

Yoori Cho¹, Dowon Lee¹ and SoYeon Bae^{2*}

Abstract

Background: Though the biomass of floral vegetation in understory plant communities in a forested ecosystem only accounts for less than 1% of the total biomass of a forest, they contain most of the floral resources of a forest. The diversity of understory honey plants determines visitation rate of pollinators such as honey bee (*Apis mellifera*) as they provide rich food resources. Since the flower visitation and foraging activity of pollinators lead to the provision of pollination service, it also means the enhancement of plant-pollinator relationship. Therefore, an appropriate management scheme for understory vegetation is essential in order to conserve pollinator population that is decreasing due to habitat destruction and disease infection. This research examined the diversity of understory honey plant and studied how it is related to environmental variables such as (1) canopy density, (2) horizontal heterogeneity of canopy surface height, (3) slope gradient, and (4) distance from roads. Vegetation survey data of 39 plots of mixed forests in Chuncheon, Korea, were used, and possible management practices for understory vegetation were suggested.

Results: This study found that 113 species among 141 species of honey plant of the forests were classified as understory vegetation. Also, the understory honey plant diversity is significantly positively correlated with distance from the nearest road and horizontal heterogeneity of canopy surface height and negatively correlated with canopy density.

Conclusions: The diversity of understory honey plant vegetation is correlated to vegetation structure and human impact. In order to enhance the diversity of understory honey plant, management of density and height of canopy is necessary. This study suggests that improved diversity of canopy cover through thinning of overstory vegetation can increase the diversity of understory honey plant species.

Keywords: Apis mellifera, Forest ecology, Airborne LiDAR, Pollination service, Vegetation structure

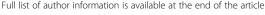
Background

Effects of pollinators on plant community have been widely studied since pollination was recognized as a good example of an ecosystem service, providing not only an economic benefit (Ricketts et al. 2008) but also basic life-support processes (Daily 2000). As about 80% of wild plant species rely on insect pollination for fruit and their reproduction, pollinator declines can cause a great loss in pollination services, which could significantly harm the ecosystem stability (Potts et al. 2010). Especially, honey bees (*Apis mellifera*) affected by colony collapse disorder (CCD), a recent, pervasive phenomenon

in Northern Hemisphere, are of concern in terms of conservation. Although there has been little study that proves the causes for the collapse of honey bee colonies (Hadley and Betts 2012; Wratten et al. 2012), parallel declines of plant and pollinator relationship in a large scale highlight the need for management of plants as resources for pollinators (Hadley and Betts 2012).

Among a number of insect pollinators, bees are the most significant anthophiles that are well adapted to the environment (Kevan and Baker 1983). Flowers are important food resources for both larvae and adult bees, their pollen and nectar are needed for raising young and their own overwintering (Kevan and Baker 1983). Therefore, maintaining the pollination services can be achieved by the conservation and management of enough resources for pollinators (Ricketts et al. 2008). One important factor

²Division of Ecological Survey Research, NIE, 1210 Geumgang-ro, Seocheon-gun 33657 Seoul, South Korea





^{*} Correspondence: baelovejx@gmail.com

for the diversity and abundance of pollinator populations is the composition of floral communities (Hegland and Boeke 2006).

The understory floral vegetation in vascular and nonvascular plants accounts for most of the plant species diversity in forested ecosystems, and anthophilous insects use flowers from these plants for their food (Proctor et al. 2012). Understory vegetative layer hardly covers 1% of the biomass of the forest but has 90% or more of the plant species that represents the majority of floristic diversity of the ecosystem (Proctor et al. 2012; Gilliam 2007). For these reasons, well-planned management scheme that understands the mechanisms maintaining diversity of understory vegetation can play a key role in conserving declining pollinators. A number of environmental factors inside and outside a forest can have an influence on richness of understory vegetation. For example, highly diverse understory vegetation could be a result of intra-stand heterogeneity due to differences in availability in limiting resources such as nutrient, light, and water (Huebner et al. 1995). Therefore, a sufficient presence of stands that are dominated by overstory species through management could be an important way to sustain the diversity of understory species (Fourrier et al. 2015).

According to Ebeling et al. (2008), visitation rates of pollinators linearly increased with the degree of blooming of flowers and the number of bloomed flowers in a particular plant community. However, existence of plants that are known to be favored by pollinators in general did not have a significant effect on richness of pollinators. This result indicates that planting abundant honey plants only is not enough to protect pollinator species, but there needs to be something more complicated and policy makers and conservationists should consider environmental variables. Honey plants, in this study, are defined as plant species that produce nectar required by honey bees. Bees collect nectar and convert it into honey which is the primary food source for maintenance of their colony.

This study is to quantify and compare understory honey plant diversity among sampled plots in Chuncheon, South Korea, and to determine how this diversity was related to different environmental variables, in particular vegetation structure, topography, and human impact. Then, we suggest a possible forest management scheme for pollinator conservation as an implication of this study.

Methods

Study site

This study was conducted in temperate mixed forests in Chuncheon (37° 55′ N, 127° 52′ E), South Korea (Fig. 1). It is located in Gangwon province, approximately 90 km east of Seoul. The forests of the study area have 29% of broadleaved forests cover, 30% of coniferous forests cover, and 41% of mixed forests (Bae 2015). Mongolian oak

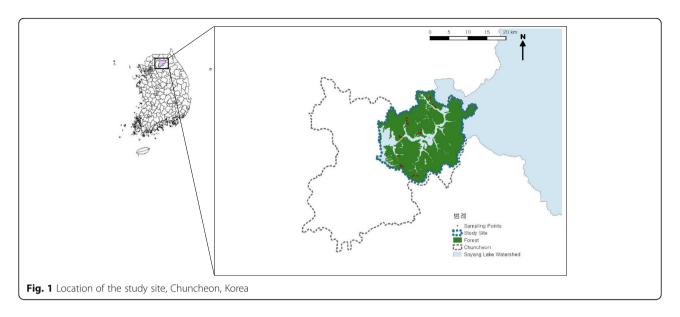
(*Quercus mongolica*) and cork oak (*Quercus variabilis*) are the dominant broadleaved species, while Japanese red pine (*Pinus densiflora*), pitch pine (*Pinus rigida*), and Korean pine (*Pinus koraiensis*) are the dominant coniferous species (Bae 2015). The area of the forests is 400.55 km², and the annual average precipitation and temperature of the study site are 1347.3 mm and 11.1 °C (information from Korea Meteorological Administration).

Environmental variables

Understory species diversity may be the results from many different environmental variables (Huebner et al. 1995). The factors selected for this study are the variables that are known to be influencing plant establishment and growth (Table 1). The environmental variables measured at each site were (1) canopy density, (2) horizontal heterogeneity of canopy surface height, (3) slope gradient, and (4) distance from roads. Airborne LiDAR (Light Detection and Ranging), a remote sensing tool for measuring threedimensional habitat structure, was adopted to measure canopy density, horizontal heterogeneity of canopy surface height, and slope gradient. GIS (geographic information system, provided by © Naver Corp.) data was also adopted to measure distances between the sampled plots and the surrounding roads. LiDAR data are comprised of coordinates and elevation and can be classified into ground and vegetation returns, so that by using the data, it is possible to measure stand structure additionally such as vertical complexity or horizontal heterogeneity. We calculated horizontal heterogeneity of canopy surface height by using a measure of spatial autocorrelation with local Geary's c. Each environmental variable has no significant correlation with another one (Spearman's rank correlation coefficient among four variables ρ < .05).

Sampling

Thirty-nine plots were sampled across the study region for calculating diversity of honey plants. Plots that are at least 200 m apart from each other were only chosen in order to control potential environmental effects. The sampling was conducted at 39 sampling points in June and September, 2014 and May 2015. Each point was sampled in a 10 × 10 m quadrant. In each sample site, species in the ground vegetation (shrubs and herbaceous plants) and the canopy cover of the tree layer were recorded. The elevation survey points below 400 m were limited. In addition, sampling sites were chosen as apart from road at least 100 m. "Overstory species" in this study means woody species of the canopy stand and "understory species" describes plants growing on the forest floor whose heights are less than 2 m, including bryophytes, herbaceous, and woody species. Honey plant identification was conducted with reference to Jang (2009).



Statistics

Statistical dependence between overall, overstory, and understory vegetation was measured with Spearman rank correlation. The generalized linear models with Poisson distribution were employed for modeling understory species diversity, since the dependent variable, species richness per plot, is count data. All the data were statistically analyzed using R (R Core Team 2015).

Results

Among 251 plant species excluding 5 unspecified species, 141 species are identified as honey plants in our study site (Table 2). The mean of occurred honey plants species number was 18.13 ± 7.48 (mean \pm SD), and most of them, 15.31 ± 7.82 (mean \pm SD), were understory honey plant (Table 3). Dominant honey plant species of understory communities were *Quercus* spp., *Corylus heterophylla*, *Castanea crenata*, *Styrax obassia*, and *Lindera obtusiloba*. The rank correlation between the overall honey plants richness and species richness of understory honey plant was 0.97 (Spearman rank correlation, p < .001) (Fig. 2). Those results indicated the overall honey plants richness were determined by the species richness of understory honey plant.

In Poisson regression, understory diversity is significantly positively correlated with horizontal heterogeneity of canopy surface height and distance from a road and negatively correlated with canopy density (Table 4).

Discussion

Canopy density and horizontal heterogeneity of canopy surface height

Canopy dynamics of overstory is a product from permanent processes of succession and disturbance, and they contribute to heterogeneity of community, meeting ecological requirements such as light, water, and nutrient (Valverde and Silvertown 1997). And it is understory vegetation that is much benefited from heterogeneity of the canopy properties. Especially, canopy gaps and the light that passed through the gaps have been considered as the most important limiting factor that affects composition and growth of understory vegetation (Lefrancois et al. 2008; Latif and Blackburn 2010). Furthermore, canopy gaps created by harvesting increase not only species diversity but also functional diversity of the understory vegetation (Kern et al. 2014). According to Walters and Stiles (1996), both floral density and pollinator visitation rates were considerably higher in patches under forest canopy gaps than patches under closed canopy.

Table 1 The environmental variables selected and description for each variable

	Environmental variables	Variable description	Mean ± SD
Vegetation structure	Canopy density (%)	Average percentage of canopy density above 2 m within 50-m radius of plot point	86.46 ± 16.34
	Horizontal heterogeneity of canopy surface height	A measure of spatial autocorrelation of maximum vegetation height with local Geary's c within 50-m radius	1.62 ± 1.19
Topography	Slope gradient (°)	Average slope gradient within 50-m radius of plot point	31.05 ± 7.30
Human impact	Distance from a road (m)	Distance to the closest road from plot point	258.79 ± 199.13

Table 2 Overall and honey plant richness of the studied sites

	Richness	Overstory	Understory	Co-occurring
Overall	251	17	210	24
Honey plant	141	9	113	19

"Overstory" and "understory" stands for the richness of plant species that were only found in each story. Among 251 plant species, 141 species are honey plants in our study site. Richness of understory honey plants accounts for 93.62% of overall honey plant richness while that of overstory accounts for only 19.86%

Canopy gaps have a positive relation with species richness of shrub layer especially (Gazol and Ibáñez 2009). In spite of some exceptions, the relationship between forest canopy gap and light transmittance are the results of complex interactions leading to denser canopy space filling and more light interception (Angelini et al. 2015). Thus, understory vegetation may receive enough amount of radiance. Different traits of forest overstory affect the creation of canopy gaps which determines light intensity in the understory. The structure of overstory is one of the characteristics mainly correlated to light availability for understory vegetation. High values of local Geary from our result are determined by significant differences between the pivotal locality and its neighbors (Sokal et al. 1998). As local Geary values were significantly positively related to understory diversity, it illustrates that sufficient canopy openings with horizontal heterogeneity of the height of overstory vegetation should be guaranteed (Fig. 3).

According to Angelini et al. (2015), when the canopy is closed and homogeneous, the passage of light through overstory vegetation relies on the characteristics of the crowns, then on overstory plant richness. When management practices open the crown cover with the same overstory richness, stand density accounts for the light availability. In our study, however, the local Geary mean value of maximum vegetation height was correlated to neither the canopy density (2-60 m, Pearson's correlation coefficient r = -0.268, p value = .099) nor species richness of overstory vegetation (r = -0.201, p value = 0.219). This result demonstrates that it is solely the heterogeneity of overstory's vertical structure, rather than its species composition or density, which plays an important role in determining understory plant's richness. It is in contrast with the examination of literatures by Angelini et al. (2015). Angelini et al. (2015) concluded that in regular mixed forests, the understory light availability such as the

Table 3 Mean and standard deviation of honey plant richness in overall, overstory, and understory layers over 39 sites

	Mean \pm standard deviation
Overall honey plant richness	18.13 ± 7.48
Overstory honey plant richness	2.82 ± 1.71
Understory honey plant richness	15.31 ± 7.82

spatial and temporal distribution of radiance are controlled by tree composition of canopy covers. The variability between conclusions may come from differences in arrangement of stems in space and their size of overstory vegetation.

Distance from a road

Roads have become an important landscape feature (Watkins et al. 2003) that may influence ecological processes in a surrounding habitat. It is still unclear how distance from roads can affect the diversity of understory vegetation in a forest, and the ecological impacts of roads and traffic, however, have become a great concern (Spellerberg 1998), especially on understory plant richness (Enoki et al. 2014). Guirado et al. (2007) studying Mediterranean forests found that the total species richness of understory vegetation increased with distance to the main roads. Pollutants affecting plants and animals range from noise, light, sand, dust to other particulates, metals, and gases (Spellerberg 1998). Also, road dust could be an important factor for plant diversity. Dust that are mobilized and spread by the road traffic can restrict photosynthesis, respiration, and transpiration of plants (Trombulak and Frissell 2000). According to Wong et al. (1984, in Watkins et al. 2003), plant materials sampled from a site with a high traffic density showed a significant decrease in root growth whereas increased root growth was found for plants sampled from low-traffic-density areas. In addition to physiological stress generated from roads, the closer the habit is to a road, the more disturbances on vegetation by human influence there may be. On the other hand, Watkins et al. (2003) found higher richness of understory vegetation on the roadside edge since lower canopy cover of the edge allows more light to reach understory. Thus, road density, vehicle transportation, and distribution of roads around the area of interest may interplay, affecting the richness of understory vegetation.

Implications

From the findings of this study, honey plant richness in understory is significantly related to canopy density and distance from the closest road. Understory light and its distribution, especially, can be controlled, at least partially, by silvi-cultural and harvesting practices according to the overstory structure (Angelini et al. 2015). Therefore, in order to enhance the diversity of understory honey plant as a pollinator conservation strategy, canopy density of overstory should be managed. Canopy gaps created by human activities such as logging could change not only micro-environmental conditions of a forest increasing understory richness but also the total bee abundance. According to Jackson et al. (2014), the number of pollinator groups was more abundant in

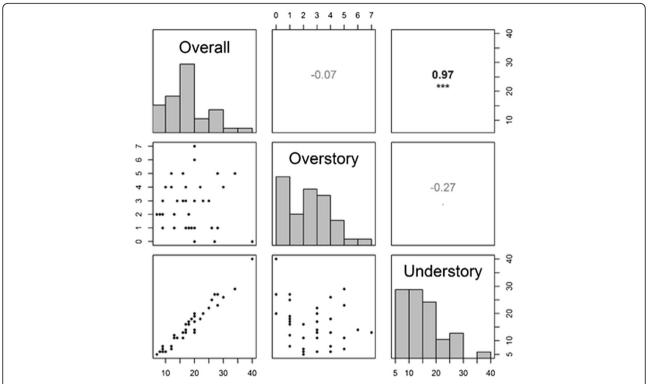


Fig. 2 Multiple displays of pairwise relationships between overall, overstory, and understory honey plant richness with Spearman rank correlation of significance levels (****p < .001)

forests that are younger and closer to logging roads, likely due to more available light and more floral resources near the roads. In a recent study by Girling et al. (2013), it was found that pollution from diesel exhaust emissions altered the constituents of a synthetic blend of floral odors. Exposure of flowers to diesel exhaust can reduce both the ability of honey bees to navigate to the flowers and efficacy of pollination services they provide.

In addition to management of canopy gaps, planting diverse honey plant species is certainly a supplementary strategy for pollinators like honey bee since existence of diverse species guarantee different flowering dates. So planting diverse species and increasing the understory richness for pollinator improves functional diversity of a forest, making it more stable and resilient in different

Table 4 Poisson regression with understory diversity (species richness) as the dependent variable and environmental variables included as independent variables. n = 39, p value $\leq .05$ level of significance

Variables	В	Wald χ^2	p value
Canopy density	-1.033	50.267	<.000
Horizontal heterogeneity of canopy surface height	0.188	38.785	<.000
Slope gradient	-0.404	1.568	.211
Distance from a road	0.001	8.302	.004

blooming periods of understory vegetation (McCann 2000). Blossom density, however, could be more significant than plant richness in explaining pollinator activity (Hegland and Boeke 2006). Also, a forest habitat that provides only a few floral resources, i.e., limited number of honey plants, may be inadequate to nurture healthy bees (Vaudo et al. 2013). Bees can self-select their own food to satisfy their requirements, so that they will be negatively affected if various foraging choices and diets are not guaranteed throughout their lives (Vaudo et al. 2013).

According to the Korea Beekeeping Association (Korea Beekeeping Association 2007), plant species that were selected for governmental honey plant planting scheme were all tree species such as Quercus acutissima, Betula platyphylla var. japonica, Fraxinus rhynchophylla, and *Liriodendron tulipifera* for better honey harvesting and eventually for economic purposes. However, it is still not obvious how trees can contribute to conservation of pollinators. Roubik (1993) in his research hypothesized that bees either like to forage in the canopy or specialize there. The results showed that the data obtained in a long term did not prove the hypothesis, except for the nocturnal Megalopta and one stingless bee, Partamona, for 20 species and 10 genera including A. mellifera. This demonstrates that bees are quite opportunistic and unpredictable (Roubik 1993).

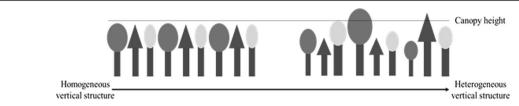


Fig. 3 Illustration that conceptualizes local Geary mean value of maximum vegetation height. As the vertical structure of vegetation of a plot is more heterogeneous, local Geary mean is higher than less heterogeneous that the other

Overstory vegetation like understory vegetation also provides abundant floral resources for pollinators; fluctuations of floral resources, however, highly vary every year (Inari et al. 2012). This temporal discrepancy in floral resources may affect pollinator population (Inari et al. 2012). However, the flowering days of understory species is longer than that of overstory tree species, lasting from early spring to autumn (Inari et al. 2012).

Yet, there are still limitations of this study. Light availability for understory vegetation varied by canopy structures is one of the most important factors in this study. Light transmittance, however, significantly varies among tree species, and it depends on their light demands and shade tolerance (Inari et al. 2012). The composition of understory vegetation can be more related to their trait of shade tolerance than canopy gaps (Kern et al. 2014), regardless of whether or not they are the plants that pollinators favor.

In addition, the effect of slope aspect on the diversity of understory vegetation was not considered due to the lack of the number of samples. Slop aspect, however, is inherently related to available light and soil moisture, which should be discussed in detail. In general, understory vegetation shows high species richness and alpha diversity when it is shed on south-facing slope (Messier et al. 1998; Valladares and Niinemets 2008). In Northern Hemisphere, south-facing slope usually has higher temperature and light intensity and lower humidity with a more variable microclimate (Auslander et al. 2003). Still, there is no consensus agreed between authors on which aspect vegetation develops. It is more dependent on regions. According to a study conducted at Mt. Jumbong, South Korea, high productivity and species diversity on north-facing slope having less evaporation rate since water use efficiency was one of the most important limiting factors for plant growth in Korea. Therefore, the relationship between understory diversity and slope aspect in our study may be because understory vegetation has a higher evaporation rate, so that plant species on south-directed slopes could be under stress due to the higher atmospheric moisture demand (Huebner et al. 1995). South-directed slopes are expected to have six times higher solar radiation than north-directed slope (Auslander et al. 2003). Slopes facing south retain flora that are more tolerant to stress and demand more light, which is revealed by long-term monitoring (Bennie et al. 2006; Gong et al. 2008). Although located only a few hundred meters apart, the microclimatic conditions generated by different slope aspects could vary dramatically. Between slopes, a sharp microclimatic gradient can stress the plants (Auslander et al. 2003) and their pollinators. Thus, differences and diversity in species composition on different slope aspects were explained by resource availability. Another possible explanation for higher understory vegetation is different pedologic processes. The difference of vegetation composition and productivity, and erosion processes of soil are generally accentuated on slopes facing south (Rech et al. 2001), which leads to contrasting soil characteristics of north- and south-directed slopes (Gong et al. 2008).

Although the findings of this study are meaningful, understory vegetation richness in general can be explained by intermediate disturbance hypothesis. As stated above, partially removing overstory canopy can create more growing space and release more resources that are available and therefore have a positive effect on understory plant diversity. Again, this means that opening canopy gaps as much as possible by managing canopy density is not a definite solution for enhancing understory honey plant richness. Like the local Geary value illustrated, sufficient canopy openings with horizontal heterogeneity of height of overstory vegetation should be the first to be considered.

For further research, spatial and temporal variability of understory light determined by not only gaps but also other qualitative and quantitative attributes of canopy cover such as heterogeneity of stand spacing and characteristics of crowns should be studied. The causal relationship between the actual amount of pollutants from roads and the growth of understory vegetation should be further studied as well. Pollination efficiency measured by richness and abundance of pollinators in the study site should also be empirically examined to validate the findings of this study. Also, collecting and statistically examining more slope aspect data will contribute to the findings of this study.

Conclusions

The floral vegetation in understory plants community in forested ecosystems plays an important role as the main food source for pollinators such as honey bees. This research shows that vegetation structure and human impact such as distance to roads are correlated to the diversity of understory honey plant. This study suggests that management of density and height of canopy is necessary in order to improve the diversity of understory honey plant.

Acknowledgements

We sincerely thank Minjoo Lee of the National Institute of Forest Science and Dr. Engkyong Lee of Teoal for their contribution in developing this paper. We greatly acknowledge Dr. Wanmo Kang of the Korea Environment Institute, Ho Choi of Seoul National University, and Hyo-In Lim of the National Institute of Forest Science for exerting much effort for the field work of this research. We also would like to thank the National Forest Management Office at Chuncheon for their cooperation throughout the study period and two anonymous reviewers for their valuable comments.

Funding

This research was supported by the Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (NRF-2013R1A1A2012874) and through the 4th National Ecosystem Survey by the National Institute of Ecology.

Availability of data and materials

Not applicable.

Authors' contributions

YC and SYB undertook the statistical analysis and drafted the manuscript. SYB also participated in collecting the field data for the vegetation surveys. DL assisted in the data collection (vegetation surveys) and contributed in the discussion of this study. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Consent for publication

Not applicable.

Ethics approval and consent to participate

Not applicable.

Author details

¹Department of Environmental Planning, Seoul National University, 1 Gwanak-ro, Seoul 08826, South Korea. ²Division of Ecological Survey Research, NIE, 1210 Geumgang-ro, Seocheon-gun 33657 Seoul, South Korea.

Received: 10 August 2016 Accepted: 6 December 2016 Published online: 12 January 2017

References

- Angelini, A., Corona, P., Chianucci, F., & Portoghesi, L. (2015). Structural attributes of stand overstory and light under the canopy.
- Auslander, M., Nevo, E., & Inbar, M. (2003). The effects of slope orientation on plant growth, developmental instability and susceptibility to herbivores. *Journal of Arid Environments*, 55, 405–416.
- Bae, S. Y. (2015). Modelling avian taxonomic, functional, and phylogenetic diversity in relation to 3-D forest structure. Seoul: PhD dissertation, Seoul National Univ.
- Bennie, J., Hill, M. O., Baxter, R., & Huntley, B. (2006). Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology*, *94*, 355–368.
- Daily, G. C. (2000). Management objectives for the protection of ecosystem services. *Environmental Science & Policy, 3, 333–339*.

- Ebeling, A., Klein, A. M., Schumacher, J., Weisser, W. W., & Tscharntke, T. (2008). How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos, 117*, 1808–1815.
- Enoki, T., Kusumoto, B., Igarashi, S., & Tsuji, K. (2014). Stand structure and plant species occurrence in forest edge habitat along different aged roads on Okinawa Island, southwestern Japan. *Journal of Forest Research, 19*, 97–104.
- Fourrier, A., Bouchard, M., & Pothier, D. (2015). Effects of canopy composition and disturbance type on understorey plant assembly in boreal forests. *Journal of Vegetation Science*, 26, 1225–1237.
- Gazol, A., & Ibáñez, R. (2009). Different response to environmental factors and spatial variables of two attributes (cover and diversity) of the understorey layers. Forest Ecology and Management, 258, 1267–1274.
- Gilliam, F. S. (2007). The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience*, *57*, 845–858.
- Girling, R. D., Lusebrink, I., Farthing, E., Newman, T. A., & Poppy, G. M. (2013). Diesel exhaust rapidly degrades floral odours used by honeybees. *Scientific Reports*, 3, 2779.
- Gong, X., Brueck, H., Giese, K., Zhang, L., Sattelmacher, B., & Lin, S. (2008). Slope aspect has effects on productivity and species composition of hilly grassland in the Xilin River Basin, Inner Mongolia, China. *Journal of Arid Environments*, 72, 483–493.
- Guirado, M., Pino, J., & Roda, F. (2007). Comparing the role of site disturbance and landscape properties on understory species richness in fragmented periurban Mediterranean forests. *Landscape Ecology*, 22, 117–129.
- Hadley, A. S., & Betts, M. G. (2012). The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biological Reviews*, 87, 526–544.
- Hegland, S. J., & Boeke, L. (2006). Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology*, 31, 532–538.
- Huebner, C. D., Randolph, J., & Parker, G. (1995). Environmental factors affecting understory diversity in second-growth deciduous forests. *American Midland Naturalist*, 155–165.
- Inari, N., Hiura, T., Toda, M. J., & Kudo, G. (2012). Pollination linkage between canopy flowering, bumble bee abundance and seed production of understorey plants in a cool temperate forest. *Journal of Ecology*, *100*, 1534–1543.
- Jackson, M. M., Turner, M. G., & Pearson, S. M. (2014). Logging legacies affect insect pollinator communities in Southern Appalachian Forests. Southeastern Naturalist, 13, 317–336.
- Jang, J. W. (2009). A study on honey plants in Korea. Daegu: PhD Dissertation, Daegu Univ.
- Kern, C. C., Montgomery, R. A., Reich, P. B., & Strong, T. F. (2014). Harvest-created canopy gaps increase species and functional trait diversity of the forest ground-layer community. Forest Science, 60, 335–344.
- Kevan, P., & Baker, H. (1983). Insects as flower visitors and pollinators. *Annual Review of Entomology*, 28, 407–453.
- Korea Beekeeping Association. (2007). Current status of honey plant afforestation. Korea Beekeeping Bulletin, 331, 52–23.
- Latif, Z. A., & Blackburn, G. A. (2010). The effects of gap size on some microclimate variables during late summer and autumn in a temperate broadleaved deciduous forest. *International Journal of Biometeorology*, 54, 119–129.
- Lefrancois, M.-L., Beaudet, M., & Messier, C. (2008). Crown openness as influenced by tree and site characteristics for yellow birch, sugar maple, and eastern hemlock. *Canadian Journal of Forest Research*, *38*, 488–497.
- McCann, K. S. (2000). The diversity–stability debate. *Nature*, 405, 228–233.
- Messier, C., Parent, S., & Bergeron, Y. (1998). Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *Journal of Vegetation Science*, 9, 511–520.
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25, 345–353.
- Proctor, E., Nol, E., Burke, D., & Crins, W. J. (2012). Responses of insect pollinators and understory plants to silviculture in northern hardwood forests. *Biodiversity and Conservation*, 21, 1703–1740.
- R Core Team. (2015). R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.
- Rech, J. A., Reeves, R. W., & Hendricks, D. M. (2001). The influence of slope aspect on soil weathering processes in the Springerville volcanic field, Arizona. *Catena*, 43, 49–62.
- Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., & Mayfield, M. M.

- (2008). Landscape effects on crop pollination services: are there general patterns? *Ecology Letters*, *11*, 499–515.
- Roubik, D. W. (1993). Tropical pollinators in the canopy and understory: field data and theory for stratum "preferences". *Journal of Insect Behavior*, *6*, 659–673.
- Sokal, R. R., Oden, N. L., & Thomson, B. A. (1998). Local spatial autocorrelation in a biological model. *Geographical Analysis*, 30, 331–354.
- Spellerberg, I. (1998). Ecological effects of roads and traffic: a literature review. Global Ecology and Biogeography, 7, 317–333.
- Trombulak, S. C., & Frissell, C. A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology, 14*, 18–30.
- Valladares, F., & Niinemets, U. (2008). Shade tolerance, a key plant feature of complex nature and consequences. Annual Review of Ecology, Evolution, and Systematics. 39, 237–257.
- Valverde, T., & Silvertown, J. (1997). Canopy closure rate and forest structure. Ecology, 78, 1555–1562.
- Vaudo, A. D., Tooker, J. F., Grozinger, C. M., & Patch, H. M. (2013). Bee nutrition and floral resource restoration. *Current Opinion in Insect Science*, 10, 133–141.
- Walters, B. B., & Stiles, E. W. (1996). Effect of canopy gaps and flower patch size on pollinator visitation of Impatiens capensis. *Bulletin of the Torrey Botanical Club*, 184–188.
- Watkins, R. Z., Chen, J., Pickens, J., & Brosofske, K. D. (2003). Effects of forest roads on understory plants in a managed hardwood landscape. *Conservation Biology*, 17, 411–419.
- Wong, M., Cheung, L., & Wong, W. (1984). Effects of roadside dust on seed germination and root growth of Brassica chinensis and B. parachinensis. *Science of the Total Environment, 33,* 87–102.
- Wratten, S. D., Gillespie, M., Decourtye, A., Mader, E., & Desneux, N. (2012).
 Pollinator habitat enhancement: benefits to other ecosystem services.

 **Agriculture Ecosystems & Environment, 159, 112–122.

Submit your next manuscript to BioMed Central and we will help you at every step:

- We accept pre-submission inquiries
- Our selector tool helps you to find the most relevant journal
- We provide round the clock customer support
- Convenient online submission
- Thorough peer review
- Inclusion in PubMed and all major indexing services
- Maximum visibility for your research

Submit your manuscript at www.biomedcentral.com/submit

