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INVITED ORIGINAL RESEARCH PAPER

Effect of forest clear cuts on plant–pollinator interactions: the case of three ericaceous subshrubs in Lithuanian pine forests

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Abstract
Managed boreal pine forests are subject to regular clear cuts causing significant disturbances to these ecosystems. It is believed that, to some extent, they resemble natural cycles of forest growth, decline, and regeneration and can benefit, e.g., mutualistic relations among plants and pollinators. To study the impact of forest management (clear cuts) on pollinator visitation, we focused on three ericaceous plant species, *Vaccinium myrtillus*, *V. vitis-idaea*, and *Calluna vulgaris*, common elements of pine forest understory. Our observations, conducted in Lithuania, showed that there are no differences among control mature stands and clear cut areas in terms of visitation frequency for all three studied species. However, at least for *C. vulgaris*, a shift toward fly visits was observed in the clear cut site, showing that open areas are preferred habitats for these insects. Ants constituted an important share of visitors to flowers of *V. myrtillus* and *C. vulgaris*, suggesting their important role in reproduction of these plant species.

Keywords
biodiversity; boreal forest; *Calluna*; Ericaceae; forest management; *Pinus sylvestris*; pollination; *Vaccinium*

Introduction

Mutualistic interactions forming large and complex networks of reciprocally beneficial interactions and connecting dozens or even hundreds of species are regarded as "architecture of biodiversity" [1]. Especially pollination of flowers by animals, which involves approximately 90% of all angiosperm species [2] and a significant fraction of invertebrate animals [3], is believed to play a crucial role in generating and sustaining the biodiversity of terrestrial ecosystems. Even boreal forest ecosystems occupying northern parts of Europe, formed chiefly by gymnosperm tree species and rather poor in flowering species, are home to many zoogamous plants and invertebrate pollinators that sustain a considerable part of forest biodiversity [4]. Apart of ecosystem stability, the sustainability of the pollination process can have a direct effect on economically important plants affecting crop production [5]. In European boreal forests, such species include, e.g., those of the Ericaceae family, especially species of the genus *Vaccinium* (e.g., *V. myrtillus* L. and *V. vitis-idaea* L.), which, together with *Calluna vulgaris*, are common and abundant elements of boreal ecosystems. Apart from the biological and ecological importance (see e.g., [6,7] and references cited), they provide significant socioeconomic services, in the case of *Vaccinium* spp. being traditional wild edible forest food in many European countries [8–10] and a source of many important nutritional compounds in human diet [11–14], while in the case of *Calluna sylvestris* an important forest species in honey production [15]. Limited pollinator services in these species can lead to a decrease in fruit production [16,17], which further can deteriorate plant population stability. The level of pollination services depends on many factors, one of them being habitat disturbances [18]. In natural boreal forests, this includes biotic disturbances, fires, and windbreaks [19,20], and in managed forests occupying the majority of boreal regions such disturbances may be caused by standard management practices, e.g., clear cuts. In the opinion of some authors, to some extent they reflect a part of the natural cycle of the forest and can have beneficial effects on some groups of pollinator fauna [4]. Such positive effects of early successional stages of forest regeneration were, for instance, reported for Japan [21] and Sweden [22]. However, this may in fact be a simplistic view of variable and complex character of disturbance cycles in natural forest [19], since a recent analysis showed negative effect of human-induced disturbances on pollination in forests [23]. Therefore, to contribute to this discussion, we studied the impact of forest management (clear cuts) on pollinator visitation to flowers of common species from pine forest understory and hypothesized that forest management would significantly affect pollinator activity to these plants.

Material and methods

Study plants

We focused on three ericaceous subshrub species: *Calluna vulgaris* L. (common heather), *Vaccinium myrtillus* L. (blueberry, bilberry) and *V. vitis-idaea* L. (lingonberry), which are common elements of North European conifer forest understory [6,7].

All three species are entomophilous, pollinated by bees and other insects, and can be characterized by generalist pollination systems [4,6,7,24–27]. Pollination in *C. vulgaris* can also occur via wind-dispersed pollen [7]. Our study plants exhibit mixed-mating systems [7,26], but in all three species insect pollination is important for seed production, and both *V. myrtillus* and *V. vitis-idaea* may be pollen limited [16,17] and can produce fruit of inferior quality if self-pollinated [27].

Study sites

We chose three forest complexes in S Lithuania (forest districts Dainavos and Kuro) and E Lithuania (forest district Labanoro), and in each of them we established two sites: a recently cleared area (a clear cut in the winter preceding the survey) and, at a distance not greater than 1 km, a control area (>10 ha) of mature pine forest situated in the same soil and climatic conditions (Tab. 1). In each complex, pollinator observations were conducted simultaneously in the clear cut and control sites.

Field observations

Field observations of floral visitors were completed in 2016. The dates of field observations coincided with the peak flowering period of our study plants and observations took place in May for *Vaccinium* species and in August for *C. vulgaris*.

To record insect activities, we used digital video cameras, which is a standard procedure in many similar studies (see, e.g., [28–31]). For each site, we completed at least 12 rounds of observations on both clear cut and mature stands (six on each). Following similar studies [28,29,31], we divided each round into two phases: random choice of a patch of flowering plants (5–15 flowers on 2–3 plants) and video recording (15 min, using a digital video camera).

Tab. 1 Location of study sites.

	Region	Clear cut	Control	Clear cut area (ha)	Plant species observed
Dainavos	S Lithuania	N 54°11′532″ E 24°32′819″	N 55°16′892″ E 25°45′963″	10.3	*V. myrtillus*, *V. vitis-idaea*
Kuro	S Lithuania	N 54°56′542″ E 23°34′021″	N 54°56′516″ E 23°33′940″ N 54°56′486″ E 23°33′951″	2.1	*V. myrtillus*
Labanoro	E Lithuania	N 55°16′945″ E 25°45′865″	N 55°16′892″ E 25°45′963″	1.2	*C. vulgaris*

On each study day, observations commenced at 1000 hour and ended at 1600 hour, the latest being a peak time of insect activity for most diurnal pollinators in forests [32]. No more than six were completed in a single day, which means that for a single site observations lasted at least 2 full days or longer since during inclement weather (strong winds or rain) observations were halted and recommenced on subsequent days. Apart of video recording, we sampled floral visitors by slowly walking for 15 min along a random transect and netting insects with an entomological net or directly to plastic vials.

Later in the lab, the recordings were analyzed for the number of visits by particular insects. Since video techniques generally do not allow for precise identification of insects, we assigned them to broad functional groups: honeybees, bumblebees, solitary bees, wasps, ants, muscid flies, syrphid flies, butterflies, and beetles. The remaining insects, if present, were treated as “other”.

Statistics

Statistica 7.1 (StatSoft Inc. 2005, USA) was used for statistical calculations. For comparing insect visitation in control and clear cut sites, we applied GLMM procedure; in the case of *V. myrtillus*, the study area was treated as random effect.

Results

Vaccinium myrtillus was the first species to flower in the study year. Our transect walks revealed that flowers of *V. myrtillus* were visited mostly by hymenopterans: social bees (*Bombus terrestris*, *B. pratorum*, *B. pascuroum*, *B. hypnorum*), solitary bees (*Andrena* sp., *Andrena* cf. *jacobi*), ants, and wasps (Vespidae), and also by dipterans (hoverflies Syrphidae); however, most of video-recorded visits (over 95%) were by ants (Formicidae), which fed on nectar. In Dainavos, overall visit frequency to flowers of *V. myrtillus* was three times lower than in Kuro, 0.5 ±1.4 and 1.5 ±2.0 visits / patch / 15 min, respectively. In both cases, we observed slightly higher visit frequency to the clear cut site; however, GLMM analysis performed on pooled data for both sites showed that the difference in visitation between control and clear cut sites was statistically non-significant [Fig. 1; mixed model ANOVA $F(1, 50) = 2.7930$, $p = 0.1$].

Vaccinium vitis-idaea was observed only in Dainavos. Visits were performed by solitary bees of the genus *Andrena*. Overall, visit frequency to flowers was low (0.3 ±0.5 visits per patch per 15 min) and slightly higher in the mature forest variant (Fig. 2). However, similarly to the results for *V. myrtillus*, the differences were non-significant [mixed model ANOVA $F(1, 10) = 0.5490$, $p = 0.55$].

The highest visit frequency (4.9 ±2.7, mean and *SD*) and most diversified pollinator assemblage were recorded for *C. vulgaris*. This included social bees (*A. mellifera* and *Bombus* sp.), solitary bees (*Andrena* sp.), ants, sphecid and true wasps, ichenumonids, butterflies (*Polygonia c-album*; Nymphalidae), and flies from the family Calliphoridae and Syrphidae. Although in this case we also found no differences between two site

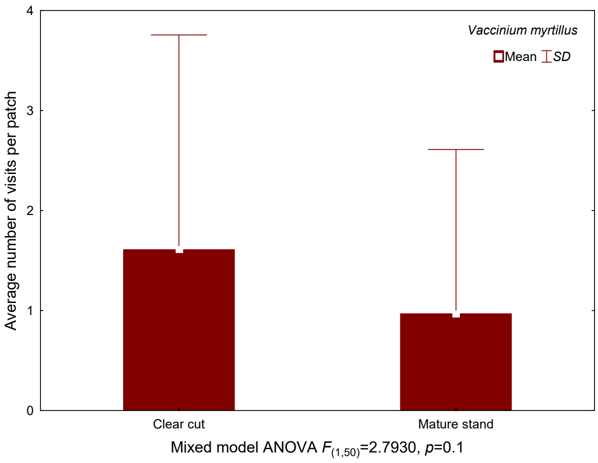

Fig. 1 Visit frequency (number of visits per patch per 15 min) to flowers of *Vaccinium myrtillus* in clear cut vs. mature pine stands, pooled data for two study sites, Dainavos and Kuro.

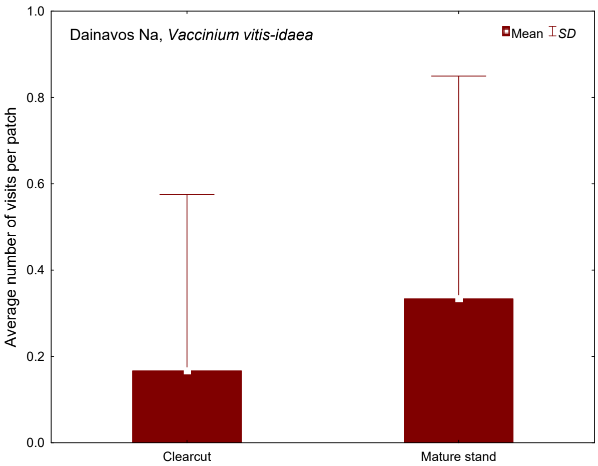

Fig. 2 Visit frequency (number of visits per patch per 15 min) to flowers of *Vaccinium vitis-idaea* in clear cut vs. mature pine stands in the Dainavos study site.

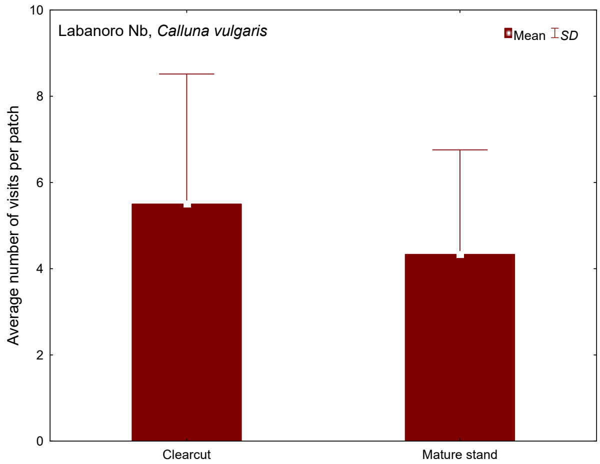

Fig. 3 Visit frequency (number of visits per patch per 15 min) to flowers of *Calluna vulgaris* in clear cut vs. mature pine stands in the Labanoro study site.

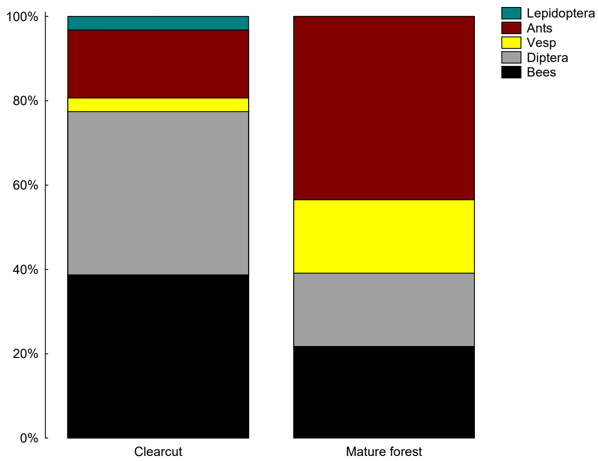

Fig. 4 Proportion of insect visits to flowers of *Calluna vulgaris* in the control (mature forest; in total 33 insects observed) and experimental site (clear cut; in total 26 insects observed) in the Labanoro forest district (E Lithuania).

variants for total visits [mixed-model ANOVA: $F(1, 10) = 0.5457$, $p = 0.48$; Fig. 3), for flies we detected increased visit frequency in clear cuts [$F(1, 10) = 5.0$, $p = 0.049$).

However, regarding the proportion of visits, the clear cut site was visited more often by bees and flies, whereas ants prevailed in the mature stand (Fig. 4).

Discussion

Contrary to our expectations, we found no (*Vaccinium* sp pl.) or very weak (*C. vulgaris*) evidence that clear cuts influence pollinator visitation patterns. Such influence was reported by Rodriguez and Kouki [6] for *V. myrtillus* and *V. vitis-idaea*. Interestingly, these authors found that the response direction is not universal, and blueberry performance and reproduction were higher in undisturbed sites, whereas lingonberry benefited from disturbance regimes. These results, however, followed a long-term experiment, where together with various levels of logging variants, fire regime was applied. Furthermore, experimental sites were generally larger (up to 8 ha) than those in our study. The beneficial effect of open spaces created by clear cuts can be related to the pace of plant cover regeneration in the cleared site. This was shown in Finland where significant positive effects on butterfly and bee abundance and diversity were observed mostly in the second year after disturbance and correlated with the flower and shrub coverage [33]. In our study, the lack of effect could therefore be connected to a low abundance and diversity of floral resources (Česonienė et al., unpublished results), since relatively recent logging negatively impacted the structure of understory vegetation with excessively short time for it to recover. Even in the case of *C. vulgaris*, increased visitation of flies to flowers of this plant does not necessarily translate into better pollination service since the response is rather weak (though significant) and, what is more important, flies are not the key pollinators of heather [24].

Nielsen and Totland [4], who studied pollination networks in boreal forests subjected to disturbances, found that clear cuts may sustain larger pollination networks with higher link diversity. This finding was generally a result of higher generalization of the species involved. According the opinion of the authors, degradation of the forest landscape induces homogenization of plant–pollinator relationships. However, in all three types of studied sites (clear cuts, young and mature forests) they found quite distinct species assemblages, overall suggesting that disturbances contribute to increased biodiversity and plant–pollinator relationships are quite robust to disturbances. Their conclusions agree with our observations that disturbances do not alter the intensity of interactions but, as in the case of *C. vulgaris*, may produce slightly different species assemblages. As shown in Nielsen and Totland [4], this may be caused by the fact that generalist plant species in one habitat type may act as specialists in other ones, which in turn could be connected to the relative abundance of flowers.

Except *V. vitis-idaea*, which in our study site was visited only by solitary bees, the remaining two species were serviced by taxonomically more diversified assemblage of pollinators. In both cases, however, the main visitors were hymenopterans, which is in agreement with earlier studies [6,7,24,25]. Interestingly, in these species a significant fraction of visits were performed by ants. Although these insects are generally regarded as inefficient pollinators and nectar thieves [34,35], they were recently reported as an important pollinator of several European taxa [36,37]. Ants were earlier recorded as floral visitors in flowers of *V. myrtillus* [25] and *C. vulgaris* [7], but treated as nectar thieves rather than efficient pollinators. In both studies, however, no measure of insect effectiveness (see, e.g., [38] for details) was applied. Ants are an important element of boreal forest ecosystems [39], and despite their low efficiency in flowers, some authors suggest that potentially they could be important in pollination of species with easily accessible flowers producing little nectar and occurring in high local densities [40], a characteristic fitting many forest Ericaceae. During our observations, we noted no destructive behavior by ants, which was reported by earlier authors [25]. They visited flowers of *V. myrtillus* and *C. vulgaris* utilizing the nectar of both species and were the most abundant visitors to flowers of blueberry, suggesting that they may contribute to pollination, at least in *V. myrtillus*. Although many authors agree that bees are the main pollinators of *Vaccinium* and *C. vulgaris* flowers ([7,24,25] and literature cited therein), since there is no experimental proof of ants' inefficiency in pollen transfer in these species, their role in pollination remains to be tested.

Despite reports of some researchers on the positive influence of forest management on biodiversity [4,6], our study revealed no differences in insect activity between managed and control forest sites. This indicates that the responses of the local arthropod communities are not necessarily universal and likely depend on factors such as remaining or recovering plant cover or time since disturbance [33]. The response can by highly dynamic and also species-specific [6], which means that further investigations are necessary to address the impact of intensive forest management on various aspects of forest biodiversity.

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Wpływ zrębów zupełnych na interakcje roślina–zapylacz: przypadek trzech krzewinek z rodziny wrzosowatych w litewskich borach sosnowych

Streszczenie

Gospodarcze drzewostany sosnowe strefy borealnej są obiektem częstych zabiegów leśnych, m.in. zrębów zupełnych, powodujących znaczące zaburzenia w tych ekosystemach. Sądzi się, że do pewnego stopnia zabiegi takie przypominają naturalne cykle wzrostu, rozpadu i regeneracji lasu i mogą pozytywnie wpływać na przykład na mutualistyczne związki pomiędzy roślinami i ich zapylaczami. Aby zbadać wpływ gospodarki leśnej (zrębów zupełnych) na odwiedziny zapylaczy skupiliśmy się na trzech gatunkach krzewinek z rodziny wrzosowatych: *Vaccinium myrtillus*, *V. vitis-idaea* i *Calluna vulgaris*, będących częstymi składnikami runa borów sosnowych. Nasze obserwacje, prowadzone na Litwie, generalnie nie wykazały istotnych różnic w zakresie częstości wizyt owadów na kwiatach trzech badanych gatunków roślin w obu siedliskach: dojrzałym lesie i zrębach. W przypadku *C. vulgaris* na siedlisku zrębowym zanotowano jednak wzrost liczebności muchówek, co może wskazywać na preferencje tych owadów w stosunku do terenów otwartych. Istotna część odwiedzin na kwiatach *V. myrtillus* i *C. vulgaris* dokonywana była przez mrówki, co sugeruje, że owady te mogą mieć wpływ na reprodukcję badanych roślin.