Plant–pollinator interactions affect colonization efficiency: abundance of blue-purple flowers is correlated with species richness of bumblebees in the Arctic

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Coevolution of efficient pollinators such as *Bombus* species (bumblebees) with the flowers they pollinate could make them spatially dependent on each other, thus affecting their distributions and abilities to colonize new areas. As *Bombus* species show a preference for blue-purple flowers, areas with a high diversity of *Bombus* species should correlate with a higher diversity of plants with blue-purple flowers. To investigate these relationships, we mapped flower colour distributions in the Arctic and tested for correlations with the richness of *Bombus* species and glaciation history. Regional occurrence and abundance of insect-pollinated species in the Arctic were obtained from the Panarctic Flora Checklist, and flower colour information for 526 species was retrieved from the literature, covering on average of 58% of each regional flora. The number of *Bombus* species within each floristic region was approximated from published distribution maps. Our results support the prediction that *Bombus* species have preference for blue-purple flower colour and that (re)colonization of species with blue-purple flowers in heavily glaciated areas is partly constrained by pollinator deficiency. Plant species with white flowers showed an opposite trend in distribution to species with blue-purple flowers. Less pollinator dependency due to alternative reproduction modes may explain the high abundance of white-coloured flowers in Arctic regions, as pigment production without the benefit of pollination to offset the energy cost may reduce fitness under marginal arctic conditions.

ADDITIONAL KEYWORDS: Arctic flora – *Bombus* – colonization – flower colour – glaciation – pollination – refugia.

INTRODUCTION

Pollination syndromes are sets of flower traits that have evolved in response to the natural selection imposed by different flower visitors (Weiss & Lamont, 1997; Fenster *et al.*, 2004). Flower colour is often one of the main traits that are affected by pollinator selection (Raine & Chittka, 2007; Schiestl & Johnson, 2013). For example, many flowers in the Northern Hemisphere appear to have evolved in order to suit the visual abilities of trichromatic pollinators, such as members of the bee genus *Bombus* which demonstrate a strong preference for flowers with blue-purple colours (Chittka & Menzel, 1992; Lunau & Maier, 1995; Briscoe & Chittka, 2001; Raine *et al.*, 2006; Lázaro, Hegland & Totland,

2008; Rausher Mark, 2008; Dyer *et al.*, 2012). Further, there is some evidence to suggest that flies have an innate preference for yellow flowers (Pickering & Stock, 2003), whereas birds seem to show a preference for pollinating red flowers (Rodriguez-Girones & Santamaria, 2004). Although the reported main colour preference among each of these pollination groups is a generalization and not absolute (Raine & Chittka, 2008; Thairu & Brunet, 2015), arguably organisms in each of these groups collectively exert some form of selective pressure upon their preferred flower traits (Swihart, 1971; Meléndez-Ackerman, Campbell & Waser, 1997; Niovi Jones & Reithel, 2001), which eventually can lead to plant speciation (Gegear & Burns, 2007).

Studies have shown that plant diversity and abundance are positively linked to pollinator diversity (Memmott, 1999; Fontaine *et al.*, 2006; Mayer *et al.*, 2012), and preferences for particular colour spectra by

certain pollinator groups may affect spatial patterns of flower colours (Aldridge & Campbell, 2009). Several arctic regions have few or no representatives of more efficient pollinators like bees or bumblebees (*Bombus* spp.), of which many have specialized structures for pollen transport (Willmer, 2011). Rather, the pollinator guilds present in the Arctic are dominated by the members of the insect order Diptera, such as flies and midges. Most Diptera species are regarded as generalist pollinators, but with some preference for yellow and white flowers (Pickering & Stock, 2003). Unusually large proportions of white and yellow flowers are present in the high Arctic of Canada (Kevan, 1972b), along with low abundances of ultraviolet (UV)-reflecting flowers (Kevan, Chittka & Dyer, 2001), which might be related to the paucity of *Bombus* species and prevalence of Diptera in this system (Willmer, 2011).

Such biogeographic patterns in flower colours as seen in Canada may relate to the glaciation history of the Arctic throughout the Pleistocene. The Arctic experienced large climatic oscillations and recurrent glaciations, with continental ice sheets covering most of North America and Eurasia (Hewitt, 2000; Dyke, 2004; Svendsen *et al.*, 2004). The arctic flora and fauna mostly experienced large-range expansions and contractions in response to these glaciations, and the Arctic is still in the process of being (re)colonized since the last glaciation (Hewitt, 2000; Callaghan *et al.*, 2004; Brochmann & Brysting, 2008; Franzén & Öckinger, 2011). Postglacial colonization efficiency has been, and still is, influenced by factors such as dispersal vectors, distance from refugia and reproduction system (Brochmann & Brysting, 2008; Alsos *et al.*, 2015; Pellissier *et al.*, 2016). If an insect-pollinated plant cannot reproduce through self-pollination or clonal means, then the presence or absence of efficient pollinators will play a significant part in reproductive success and thus colonization (Biesmeijer *et al.*, 2006; Albrecht *et al.*, 2012; Bommarco *et al.*, 2012). The dominance of white and yellow flowers seen in formerly glaciated areas such as Ellesmere Island (Kevan, 1972b; Dyke, 2004) may be a result of a (re)colonization process, where scarcity of certain pollinators, or changed pollinator behaviour under harsh Arctic conditions (Lundgren & Olesen, 2005), has influenced the (re)colonization of plant species with other flower colours..

In situ refugia in the Arctic that remained relatively ice-free throughout the glaciations should be less affected by mismatching of plants and pollinators. The most significant Arctic refugium was Beringia, which remained nonglaciated throughout the Pleistocene (Dyke, 2004). Beringia was a main source for (re)colonisation of both North America and Siberia when the ice-retreated (Hultén, 1937; Abbott & Brochmann, 2003; Eidesen *et al.*, 2013). The continuous history of species occupancy in this region has resulted in higher diversification and higher levels of endemism of both plants and animals (Abbott & Brochmann, 2003).

In this study, we utilize the great potential in biological records (Powney & Isaac, 2015). We aim to map the present regional distribution of flower colours in the Arctic and test the associations between regional species richness of *Bombus* and regional variation in flower colours. In particular, we aim to test the potential association between number of *Bombus* species and both the number and abundance of plant species with blue-purple coloured flowers. We also aim to evaluate any potential associations in the light of glaciation history. Based on former findings, we predict that the number of insect-pollinated plant species with blue-purple flowers in the Arctic increases with increasing number of *Bombus* species. We also hypothesize that heavily glaciated areas (areas completely, or almost completely covered by ice during the Pleistocene glaciations) will have lower richness and abundance of blue-purple flowers that are more attractive to pollinators such as *Bombus* species, as recurrent colonization of formerly glaciated areas will increase the risk of mismatch between pollinator and plant range distributions. The opposite trend is expected for nonglaciated, refugial areas such as Beringia, as the relative stability of these regions is assumed to support more efficient pollinators, and thus more species with blue-purple flowers, and in higher abundances than that is apparent in glaciated areas.

MATERIAL AND METHODS

DATA COMPILATION

A plant species list was compiled based on the Panarctic Flora (PAF) Checklist (Elven *et al.*, 2011). Families of species that were known to be non-insect-pollinated were excluded (Poaceae, Cyperaceae Juncaceae, and Betulaceae), as were the taxonomic categories of subspecies and varieties. The species abundance in each floristic PAF region (Fig. 1A) was tabulated (f: frequent, r: rare, s: scattered and b: borderline occurrence in the Arctic). Flower colour information is not given in the PAF and was therefore collected using a number of different arctic flora references (Hultén, 1968; Mossberg *et al.*, 1995; Rønning, 1996; Tolmačev, Rebristaja & Packer, 1996; Cherepanov *et al.*, 2000; Aiken *et al.*, 2007; Mossberg & Stenberg, 2008; Anderberg & Anderberg, 2011).

The observed 'colour' of a flower in the natural environment will depend on the vision system, the light quality and quantity present (Briscoe & Chittka, 2001; Chittka & Raine, 2006). Flies can see in four main colour groups – fly-blue, UV, fly-purple and fly-green (Lunau, 2014). Humans, bees (*Apis* sp.) and bumblebees
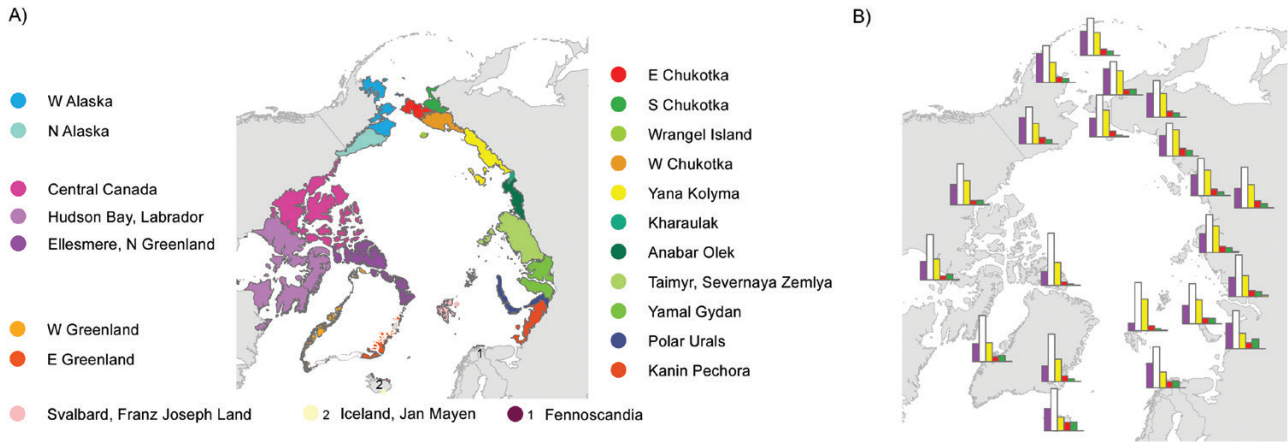
Figure 1. (A) Overview of the Panarctic Flora (PAF) regions (Elven *et al.*, 2011) and (B) the abundance of six flower colour groups (i.e. green, white, orange, yellow, red and blue-purple) for each floristic region. The outline of regions was based on CAVM Team. 2003. Circumpolar Arctic Vegetation Map http://www.ArcticAtlas.org/.

(*Bombus* sp.) can see three colour groups and have trichromatic vision. The key difference, however, is that humans see red, green, and blue wavelengths, whereas bees (*Apis* sp.) and bumblebees (*Bombus* sp.) see UV, blue and green (Srinivasan, 2009). This allows six main colour groups to be distinguished (Arnold, Savolainen & Chittka, 2009). In this study, the colours recorded by the various flora sources were categorized into six categories (i.e. green, white, orange, yellow, red and blue-purple). These records provide a very valuable indication of the flower colour spectrum present in the Arctic while recognizing that these categories are differentiated on the basis of colours as seen through human eyes and that these same colours appear differently to bees, bumblebees and other pollinators.

Colour information for each flowering species was first tallied in a presence/absence matrix. For each PAF region, the number of plant species with flowers within each of the six colour groups was counted, that is richness of plant species belonging to each colour group within each of the 21 regions. Species which have several colour morphs or combination of colours were accounted for by dividing their contribution among colours, for instance *Papaver dahlianum* have two colour morphs, then *P. dahlianum* count 0.5 to white and 0.5 to yellow. Our flora investigations had better coverage in some PAF regions than others; thus, the proportions of plant species within flower colour groups per region were calculated to avoid sampling bias (i.e. the number of plant species belonging to a given colour group was divided by the total number of species with known flower colour within that region). This measure is from now on referred to as 'species proportion'.

The presence/absence matrix was also weighted according to plant species abundance within each PAF region: frequent (*f*) = 1; scattered (*s*) = 0.5; rare (*r*) = 0.1;

borderline occurrence in the Arctic (*b*) = 0.1 [weighted the same as rare (*r*) due to similar abundance within the environment]. The weighted values for plant species abundance were summed for each PAF region, and the sum of weighted values in relation to each colour group was divided by the total weighted values for each region: [∑(weighted species) for colour X in region Y]/[∑(weighted species) for all colours in region Y] = final colour abundance for colour X in region Y (from now on referred to as 'colour abundance'). Both the species proportion and colour abundance for each PAF region were visualized using ArcGIS 10.1.

The presence/absence of *Bombus* species was derived from recorded and modelled data provided by Williams (1996) (www.nhm.ac.uk/research-curation/projects/bombus). Abundance data for *Bombus* were unfortunately not available. The number of *Bombus* species from the eight subgenera present in region 5 (Arctic) were used, and the grid squares (611 000 km²) on the map used for *Bombus* species presence were matched to each of the PAF regions (Table 1).

Glacial history was established from the literature (Hewitt, 2000; Dyke, 2004; Svendsen *et al.*, 2004), together with the descriptions provided by PAF (Elven *et al.*, 2011) where each region has been assigned to one of the three following glaciation categories: (1) heavy: majority of the region glaciated for the majority of the Pleistocene period; (2) partly: parts of the region glaciated during the Pleistocene period; and (3) non: the region was mainly nonglaciated during the Pleistocene period.

DATA ANALYSES

All data analyses were conducted in R (ver. 3.0.0, R Core Team, 2013). Summaries of the relationship between the measures of flower colour (species proportions and

Table 1. Summary of data used to evaluate relationships among flower colour, pollinator richness and glaciation history in the Arctic

Region	Glaciation	Bombus	Tot.	Tot. colour	Regional coverage (%)	Blue-purple	White	Yellow	Red	Green	Orange
Eastern Greenland	Heavy	3	98	83	84.7	22 (38)	58 (79)	32 (41)	7 (16)	8 (15)	0 (1)
Western Greenland	Heavy	2	118	84	71.2	33 (50)	67 (91)	34 (42)	7 (15)	12 (19)	0 (1)
Ellesmere Land – Northern Greenland	Heavy	2	238	152	63.9	13 (23)	45 (58)	20 (23)	4 (9)	2 (5)	0 (1)
Hudson Bay – Labrador	Heavy	4	201	128	63.7	58 (81)	93 (122)	53 (65)	11 (20)	21 (30)	0 (1)
Central Canada	Partly	13	359	225	62.7	55 (80)	88 (116)	52 (64)	10 (19)	20 (28)	0 (1)
Northern Alaska – Yukon Territory	Non	16	264	162	61.4	69 (95)	89 (118)	60 (72)	13 (23)	17 (26)	0 (1)
Western Alaska	Non	14	394	236	59.9	75 (100)	98 (125)	68 (79)	13 (24)	22 (32)	0 (0)
East Chukotka	Non	10	424	249	58.7	53 (76)	75 (97)	47 (55)	11 (21)	11 (18)	0 (1)
Wrangel Island	Partly	12	250	144	57.6	22 (36)	49 (62)	29 (33)	5 (11)	3 (7)	0 (1)
South Chukotka	Non	15	475	276	58.1	40 (57)	56 (73)	40 (48)	9 (17)	12 (19)	0 (0)
West Chukotka	Non	17	203	116	57.1	40 (59)	71 (91)	44 (52)	9 (19)	12 (20)	0 (1)
Yana – Kolyma	Non	26	194	109	56.2	34 (51)	50 (67)	35 (41)	9 (18)	15 (22)	0 (1)
Kharaulakh	Non	16	335	187	55.8	38 (56)	65 (85)	46 (54)	9 (19)	6 (13)	0 (1)
Anabar – Olenyok	Non	16	365	197	54.0	28 (43)	52 (68)	37 (43)	9 (19)	5 (11)	0 (1)
Taimyr – Severnaya Zemlya	Partly	12	290	156	53.8	39 (57)	66 (87)	48 (56)	9 (19)	15 (22)	1 (2)
Yamal – Gydan	Partly	15	245	131	53.5	35 (51)	66 (85)	38 (45)	8 (17)	14 (21)	1 (2)
Kanin – Pechora	Heavy	18	329	165	50.2	42 (62)	70 (91)	25 (31)	11 (22)	23 (32)	0 (0)
Polar Ural – Novaya Zemlya	Partly	15	322	171	53.1	39 (59)	74 (97)	42 (50)	12 (24)	19 (28)	0 (1)
Svalbard – Franz Joseph Land	Heavy	0	338	178	52.7	8 (18)	42 (55)	27 (32)	4 (10)	2 (6)	0 (1)
Northern Fennoscandia	Heavy	26	356	176	49.4	37 (56)	66 (88)	26 (34)	12 (23)	14 (23)	0 (0)
Northern Iceland – Jan Mayen	Heavy	4	323	156	48.3	26 (41)	47 (65)	19 (24)	11 (20)	14 (22)	0 (0)

Note: Region: the Panarctic Flora regions (Elven *et al.*, 2011); Glaciation: glaciation intensity within regions during Pleistocene; *Bombus*: Number of *Bombus* species (Williams, 1996); Tot: number of flowering plant species assumed to be insect-pollinated; Tot. colour: number of flowering species for which records of flower colour were obtained from the literature.* Regional coverage (%): the percentage of flowering species where flower colour data were retrieved. Subsequent columns show the distribution of species among colour groups. Species with more than one colour morph contribute to more than one colour group per region but are down-weighted according to the number of colour morphs registered for this species. The numbers listed represent sums of these weighted values, so the grand total equals the actual species number per region. Total counts of recorded colour morphs are given in parentheses.

*Hultén (1968); Mossberg *et al.* (1995); Rønning (1996); Tolmačev et al. (1996); Cherepanov *et al.* (2000); Aiken *et al.* (2007); Mossberg & Stenberg (2008); Anderberg & Anderberg (2011).

colour abundance) and number of *Bombus* species per region were calculated using a Linear Model, with flower colour as the dependent variable and *Bombus* species as the explanatory variable. Analysis of covariance (ANCOVA) was used to test for significant differences among slopes. Model outputs were summarized and presented in tables and visualized by plotting the resulting regression line on scatterplots of the two variables, *Bombus* and colour.

The relationship between abundance of flowers colours and level of glaciation within regions and between the number of *Bombus* species and glaciation level was analysed using a generalized linear model with normal error distribution, with glaciation level as the explanatory variable. Model outputs were summarized and presented in tables and data depicted as boxplots.

RESULTS

After exclusion of plant families in the PAF that were known to be pollinated by means other than by insects, our list includes 1693 species that are potentially insect-pollinated. Colour information could be reliably retrieved for 526 (31%) of these potentially insect-pollinated species from the literature. Retrieved colour information for plant species within each floristic region was on average 58% of the total for the region (range 48–85%; Table 1) and regarded to provide a representative subset of the flower colour of the arctic flora. In 128 species, more than one (two to four) colour morphs or colour variants were registered, and this variability was accounted for in our distributions (Table 1).

Species counts, species proportion and colour abundance data showed the same trend overall (Fig. 1B; Tables 1 and 2). White was the most common colour in all PAF regions (Fig. 1B; Tables 1 and 2). Blue-purple and yellow were also common colours that were found in every region, but in varying species proportion and colour abundance. Svalbard – Franz Joseph Land, a region only comprising isolated high arctic islands, had more yellow flowers than any other regions and the lowest occurrence of blue-purple flowers. Blue-purple was a common flower colour in Beringian regions like West Alaska and East Chukotka, but also Fennoscandia and Kanin Pechora had high colour abundance of blue-purple flowers (Table 2). Overall, green and red flowers were less common than blue-purple, white or yellow, and orange was rare or absent (Fig. 1B; Tables 1 and 2).

Bombus species occurred in every PAF region aside from the Svalbard – Franz Joseph Land region (Table 1). Yana-Kolyma and Fennoscandia had the highest number of *Bombus* species. The number of *Bombus* species was significantly positively correlated with blue-purple flowers using both species proportion and colour abundance (Table 3; Fig. 2). Similar tests showed no correlation related to yellow flower colour, while species proportion and abundance of white flowers showed a significant negative correlation with the number of *Bombus* species (Table 3; Fig. 2). If analysed with two analyses of covariance (ANCOVAs; one for species proportions and one for colour abundance), all slopes of the regressions are significantly different (for both species proportions and species abundance) at $P \leq 0.05$ (data not shown). However, we disregarded the results of the ANCOVAs as both white and blue-purple species proportion and white and blue-purple colour abundance seem not to be independent and were correlated (species proportion: $R^2 = 0.71$, $P = 1.04^{e-06}$, colour abundance: $R^2 = 0.55$, $P = 6.55^{e-05}$).

Species proportion and colour abundance of blue-purple flowers were significantly lower in heavily glaciated regions compared to nonglaciated regions. Partly glaciated areas had higher species proportion and colour abundance of blue-purple flowers than heavily glaciated areas, but this difference was not statistically significant (Fig 3A; Tables 4 and S1). An even stronger opposing trend was found for white flowers, with higher species proportions and colour abundances in heavily glaciated areas, while no relationship was found for yellow-coloured flowers (Tables 4 and S1). The number of *Bombus* species was significantly lower in heavily glaciated areas than in nonglaciated areas, and partly glaciated areas had fewer *Bombus* species than nonglaciated areas, but this difference was not statistically significant (Fig. 3B; Table 5).

DISCUSSION

White was the dominating flower colour in arctic regions, but also yellow and blue-purple flower colours were common (Fig. 1). Abundance of blue-purple flowers was positively correlated with the number of *Bombus* species and negatively correlated with increased glaciation intensity. White-coloured flowers showed the opposite trend to blue-purple flowers, whereas yellow-coloured flowers showed no correlation with *Bombus* species.

Flowers that appear white in the human visual spectrum are well known to dominant high altitude, high latitude and island floras (e.g. Kevan, 1972a; Campbell *et al.*, 2010; Lord, 2015). This association has previously been ascribed to a lack of specialist pollinators such as bees; however, human-white flowers that absorb UV still provide a chromatic contrast in bee-vision space (Bischoff *et al.*, 2013). Furthermore, both bees and flies have demonstrated sophisticated patterns of selectivity with respect to white versus coloured flowers (e.g. Campbell et al., 2010, 2012), so our

Table 2. Distribution of flower colours among Panarctic Flora (PAF) regions (Elven *et al.*, 2011) measured as proportions of species within flower colour groups per region (species proportion) and weighted according to plant species abundance within each PAF region (colour abundance)

Region	Species proportions						Colour abundance					
	Blue-purple	White	Yellow	Red	Green	Orange	Blue-purple	White	Yellow	Red	Green	Orange
Eastern Greenland	0.175	**0.454**	**0.251**	0.058	0.060	0.003	0.166	**0.501**	**0.237**	0.061	0.031	0.004
Western Greenland	0.214	**0.442**	**0.221**	0.043	0.077	0.002	0.189	**0.489**	**0.200**	0.052	0.066	0.004
Ellesmere Land – Northern Greenland	0.153	*0.538*	**0.236**	0.048	0.022	0.004	0.147	*0.552*	**0.242**	0.037	0.016	0.006
Hudson Bay – Labrador	**0.248**	**0.392**	0.226	0.045	0.088	0.001	0.195	**0.479**	**0.220**	0.045	0.060	0.002
Central Canada	**0.244**	**0.390**	0.231	0.045	0.088	0.001	0.215	**0.435**	**0.254**	0.045	0.048	0.003
Northern Alaska – Yukon Territory	*0.278*	**0.358**	0.242	0.052	0.068	0.001	**0.279**	**0.392**	0.215	0.070	0.044	0.000
Western Alaska	**0.271**	**0.356**	0.246	0.048	0.079	0.000	*0.302*	**0.388**	0.211	0.058	0.041	0.000
East Chukotka	**0.270**	**0.380**	0.238	0.055	0.054	0.002	**0.255**	**0.392**	0.241	0.067	0.045	0.000
Wrangel Island	0.197	**0.453**	**0.269**	0.047	0.031	0.003	0.196	**0.440**	**0.280**	0.060	0.019	0.005
South Chukotka	**0.257**	**0.357**	0.256	0.054	0.075	0.000	**0.274**	**0.352**	0.256	0.057	0.061	0.000
West Chukotka	0.226	**0.404**	**0.249**	0.053	0.067	0.002	**0.254**	**0.384**	0.252	0.065	0.042	0.003
Yana – Kolyma	0.238	**0.348**	**0.240**	0.065	0.106	0.002	0.220	**0.349**	**0.280**	0.083	0.065	0.003
Kharaulakh	0.232	**0.392**	**0.279**	0.057	0.038	0.002	0.222	**0.394**	**0.271**	0.070	0.040	0.003
Anabar – Olenyok	0.212	**0.394**	**0.282**	0.071	0.037	0.003	0.206	**0.428**	**0.244**	0.074	0.044	0.003
Taimyr – Severnaya Zemlya	0.218	**0.372**	**0.267**	0.052	0.083	0.007	0.198	**0.398**	**0.281**	0.065	0.048	0.010
Yamal – Gydan	0.218	**0.405**	**0.231**	0.051	0.085	0.008	0.204	**0.442**	**0.222**	0.065	0.051	*0.017*
Kanin – Pechora	**0.246**	**0.407**	0.146	0.065	*0.136*	0.000	**0.270**	**0.404**	0.163	0.062	*0.101*	0.000
Polar Ural – Novaya Zemlya	0.211	**0.397**	0.223	0.064	0.103	0.002	0.198	**0.426**	**0.254**	0.063	0.058	0.002
Svalbard – Franz Joseph Land	0.092	**0.504**	*0.321*	0.052	0.026	0.004	0.080	**0.507**	*0.334*	0.052	0.021	0.006
Northern Fennoscandia	**0.238**	**0.424**	0.169	0.077	0.092	0.000	**0.259**	**0.433**	0.168	0.066	0.074	0.000
Northern Iceland – Jan Mayen	0.175	**0.454**	**0.251**	0.058	0.060	0.003	**0.232**	**0.445**	0.143	*0.090*	0.090	0.003
Mean	0.220	0.411	0.242	0.055	0.070	0.002	0.217	0.430	0.237	0.062	0.051	0.003

Note: Species which have several colour morphs were accounted for by dividing their relative contribution among colour morphs. Bold numbers indicate the two largest values for species proportion and colour abundance for each region. Italicized numbers indicate the highest abundance within each colour.

Table 3. Each line represents a linear model output

	Dependent variable	Slope	SE	Intercept	SE	r^2	*P*-value
Species proportions	Blue-purple	0.003	<0.001	0.184	0.016	0.301	0.010
	White	−0.004	<0.001	0.456	0.017	0.361	0.004
	Yellow	−0.001	<0.001	0.252	0.017	0.046	0.350
Colour abundance	Blue-purple	0.004	<0.001	0.165	0.017	0.392	0.002
	White	−0.005	<0.001	0.496	0.015	0.581	<0.001
	Yellow	−0.001	<0.001	0.243	0.019	0.008	0.698

Note: The number of different *Bombus* species recorded in each Panarctic Flora region was used as predictor for the regional species proportion of each of the three common flower colours and to the regional colour abundance of each of the three common flower colours. SE: standard error.

inclusion of this colour class in our analyses of pollinator–flower correlations is justified. However, it is also likely that the dominance of white flowers in these environments also reflects the cost versus benefit of pigment-based floral signalling to available pollinators, as suggested by Campbell *et al.* (2012).

Besides white, blue-purple and yellow were the common flower colours (human visual spectrum) in the Arctic. This is in line with results reported from other regions, including the British flora (Warren & Mackenzie, 2001) and the Australian alpine flora of Mt Kosciuszko (Pickering & Stock, 2003). Arnold *et al.* (2009) reviewed flower colour along an alpine gradient in Norway by characterizing colour from an insect viewpoint but still found that purple, white and yellow flowers (human visual spectrum) were most common (Arnold *et al.*, 2009). The overall common occurrence of plant species with white, yellow and blue-purple flowers suggests that these colours attract a wide range of pollinators. Further, as the trend is similar regardless of evaluating colours from a human or insect point of view, we feel confident that flower colours as seen by humans can be used to infer relationships between flower colours and pollinators.

Red- and green-coloured flowers were far less common colours in the Arctic, and orange was rarely found. Red, green and orange flower colours have been related to specific pollinator guilds such as birds or bats (Ollerton *et al.*, 2009), dependent on interpretation and acceptance of pollination syndrome theory (Waser *et al.*, 1996). Pollinating birds and bats are not present in the Arctic, which by inference implies that red and orange flower colours would be less represented within the flora. Green flowers are rare overall among insect-pollinated species, presumably because green flowers do not stand out against background vegetation (Chittka, Thomson & Waser, 1999; Ollerton *et al.*, 2009).

Species proportion and colour abundance measures of blue-purple flowers were positively correlated with the number of *Bombus* species (Fig. 2), as expected given these more efficient pollinators prefer blue-purple flowers (Lunau, 1996; Niovi Jones & Reithel, 2001; Rausher,

2008). Although our data remain suggestive when it comes to inferring a cause-and-effect relationship, and more experimental set-ups are needed to confirm the suggested explanation, we find it unlikely that the observed correlations are mainly the result of covariation. Our results are also in line with both descriptive and experimental data from other studies, which have shown that both plant diversity and flower abundance are positively linked to pollinator diversity (Memmott, 1999; Fontaine *et al.*, 2006; Mayer *et al.*, 2012). As species proportion and colour abundance measures showed congruent results overall, for simplicity we refer to the colour abundance results in the further discussion.

White flowers showed an opposite trend to blue-purple flowers, with increasing abundance of white flowers matching decreasing number of *Bombus* species. The abundance of yellow flowers showed no correlation with *Bombus* species. This opposing trend in white-coloured flowers, and not in yellow, may be related to reproduction mode. In monocots, self-pollinated flowers are often characterized by smaller reproductive structures, no nectar and white-coloured flowers (Kennedy, 2000). Asexual or self-pollinating species have no need to attract pollinators and thus no need to produce costly colour pigments. Although pigmented flower structures may have other benefits, like heating (Song *et al.*, 2013; Little *et al.*, 2016), such structures are largely associated with attracting pollinators in order to facilitate successful sexual outcrossing (Barrett & Harder, 1996; Schiestl & Johnson, 2013). There is a well-documented trend that obligate outcrossers decrease towards the poles, whereas asexuality and self-pollination increase (Lloyd, 1980; Bierzychudek, 1985; Johnson, Smith & Rausher, 2010; Grossenbacher *et al.*, 2015). The energy budget in the Arctic is extremely tight; without the benefit of pollination to offset the energy cost, unnecessary pigment production may slightly reduce fitness (Mølgaard, 1989). This, combined with no fitness consequences from being unpigmented, might lead to frequency shifts among colour morphs (Mølgaard, 1989).
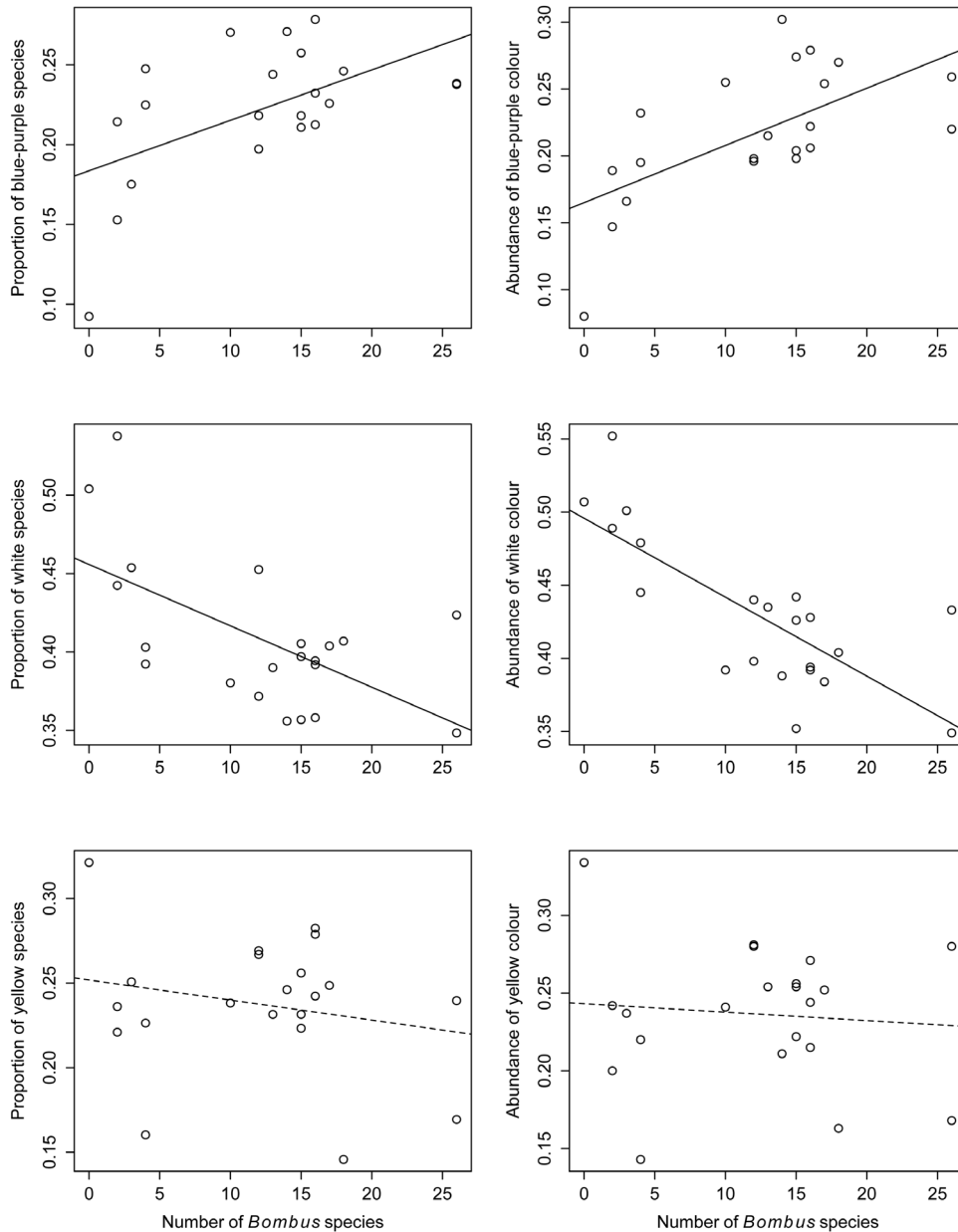
Figure 2. Visualization of Linear Model outputs between the number of *Bombus* species recorded in each Panarctic Flora region compared to the regional species proportions and to the regional abundances of each of the three common flower colours. Significant relationships are indicated by solid regression lines (see also Table 3 for each model parameters).

It seems that pollinator presence affects biogeographical patterns of flower colour, as has been shown on a local scale (Aldridge & Campbell, 2009). Nonglaciated, refugial regions, such as Beringia, showed higher levels of both *Bombus* species and blue-purple flowers compared to glaciated regions, and the numbers of both decreased with increasing level of glaciation (Fig. 3). Our patterns agree with Beringia as a major Pleistocene refugium and that this region has been shown to be a source for post-glacial (re)colonization (Hultén, 1937; Abbott & Brochmann, 2003; Eidesen *et al.*, 2013). Nonglaciated regions such as Beringia also provided an opportunity for the plants inhabiting the region to continue to flourish and evolve with mutualistic pollinators throughout glacial periods. Thus, plant–pollinator-driven *in situ* speciation is plausible in these regions and may contribute to the higher levels of both *Bombus* species and plant species with blue-purple flowers in nonglaciated areas.
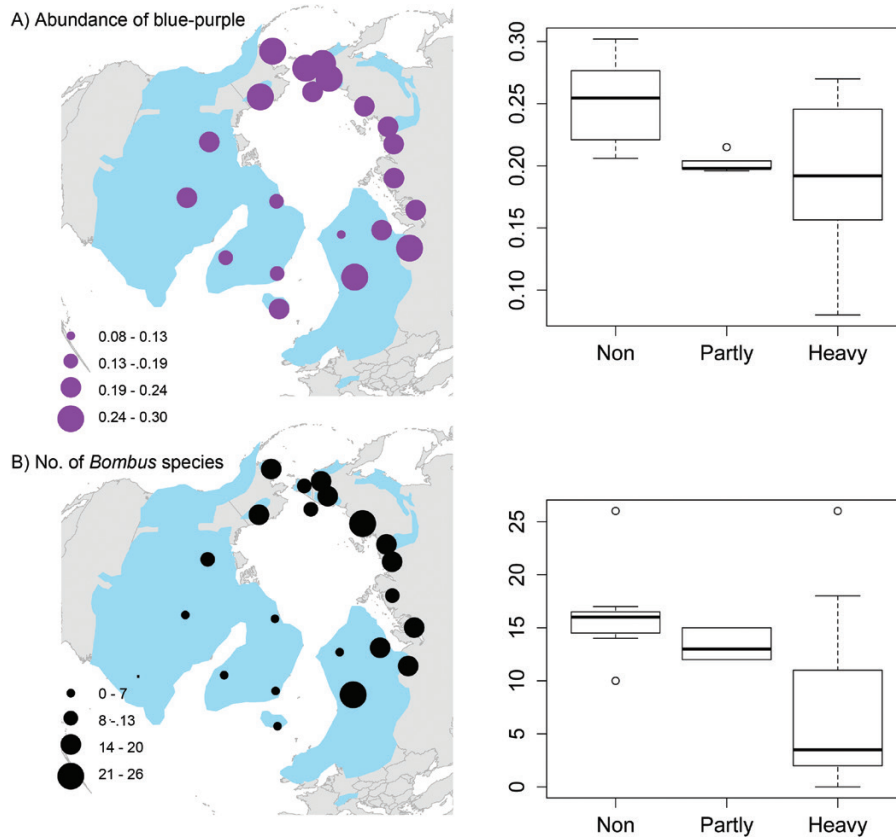
Figure 3. (A) Abundances of species with blue-purple flower colour among the Panarctic Flora (PAF) regions and boxplots showing abundance of species with blue-purple flower colour for each level of glaciation (for significant differences, see Table 4). (B) Number of *Bombus* species among Panarctic Flora regions and boxplots showing number of *Bombus* species for each level of glaciation (for significant differences see Table 5). Blue areas reflect glaciated areas during the last glacial maximum (Dyke, 2004; Svendsen *et al.*, 2004).

Table 4. Generalized linear model outputs assessing abundance of blue-purple, white and yellow flower colour in each Panarctic Flora region in relation to glaciation intensity during the last glacial maximum

	Estimate	SE	*t*-Value	Pr(>|*t*|)
Blue-purple				
Nonglaciated	0.252	0.016	16.031	<0.001
Partly glaciated	−0.049	0.025	−1.949	0.067
Heavily glaciated	−0.059	0.022	−2.671	0.016
White				
Nonglaciated	0.385	0.012	31.683	<0.001
Partly glaciated	0.043	0.020	2.212	0.040
Heavily glaciated	0.091	0.017	5.319	<0.001
Yellow				
Nonglaciated	0.246	0.015	16.475	<0.001
Partly glaciated	0.012	0.024	0.496	0.626
Heavily glaciated	−0.033	0.021	−1.555	0.137

Note: The estimate for the nonglaciated category represents the reference level of the model with its respective standard error, while the other estimates represent differences in relation to the reference level with their standard errors. SE: standard error.

Table 5. Generalized Linear Model output assessing number of *Bombus* species recorded in each Panarctic Flora region in relation to glaciation intensity during the last glacial maximum

	Estimate	SE	t-Value	Pr(>|t|)
Non-glaciated	16.250	2.304	7.052	<0.001
Partly glaciated	−2.850	3.715	−0.767	0.453
Heavily glaciated	−8.875	3.259	−2.723	0.014

Note: The estimate for the nonglaciated category represents the reference level of the model with its respective standard error, while the other estimates represent differences in relation to the reference level with their standard errors. SE: standard error.

The lowest abundance of blue-purple flowers was found in Svalbard – Franz Joseph Land, a heavily glaciated region identified as having no *Bombus* species. The main pollinators in Svalbard – Franz Joseph Land are Diptera, which tend to prefer yellow and white colours (Pickering & Stock, 2003; Chittka & Raine, 2006; Arnold *et al.*, 2009). Besides being cold-tolerant, many important dipteran families are widespread and

thus assumed to be efficient dispersers (Danks, 2004). Thus, Diptera species may colonize newly glaciated areas faster than *Bombus* species. Such dominance of Diptera in regions where *Bombus* species are few or absent may theoretically enhance the establishment of plant species with white and yellow flowers and hamper the establishment of species with blue-purple flowers. However, in contrast to the other colours, the abundance of white flowers significantly increased with increasing glaciation intensity. Thus, white-flowered species probably have an advantage during establishment that does not apply to either blue-purple- or yellow-flowered species. This difference is not readily explained by pollinator preference but might be explained by pollinator ignorance: to reproduce asexually or through self-pollination increases the probability of successful establishment and range expansion (Grossenbacher *et al.*, 2015). As argued above, the increased ability for self-pollination has been associated with white flowers (Kennedy, 2000), and this known association between white flowers and autonomous reproduction is a plausible explanation to the pattern we observe. However, we have not included reproduction mode in our data compilation and cannot test this hypothesis based on our current data.

Although the overall trend showed lower numbers of *Bombus* species and abundance of blue-purple flowers in glaciated areas, two PAF regions showed strongly deviating results. The heavily glaciated regions Fennoscandia and Kanin – Pechora showed high levels of both blue-purple flowers and *Bombus* species. Distribution patterns are shaped by a range of factors. Besides species traits and species interactions, influencing factors include the number of source regions, dispersal distance, dispersal barriers and connectivity to source regions (Alsos *et al.*, 2007; Eidesen *et al.*, 2013; Alsos *et al.*, 2015). Fennoscandia and Kanin – Pechora have probably been colonized from both southern and eastern refugia after the last glaciation (Eidesen *et al.*, 2013). Combined with good connectivity to current source areas, these factors could explain the higher number of pollinators and the retention of a larger range of blue-purple-flowered species in these regions in comparison with the other heavily glaciated regions.

We see clear trends that relate *Bombus* diversity to flower colours, but there is a substantial amount of the variation that is not explained. Although *Bombus* species have an innate preference for blue-purple flowers, they frequently also visit other flower colours. It has also been shown that *Bombus* species are fast learners that can shift colour preference, for example from blue to white if the reward is higher in the white-flowered morph than in the blue (Thairu & Brunet, 2015). Some blue-purple flowers can be efficiently pollinated by Diptera (Olesen *et al.*, 2008) however, or they have developed an alternative way of reproducing, such as self-pollination (e.g. *Pedicularis* species in Svalbard) or by utilizing an alternative pollination vector (Chittka *et al.*, 1999). There are also other factors that probably influence the distribution of flower colours in the Arctic. Advertisements to pollinators are not the sole function of flower colour in many instances (Frey, Dunton & Garland, 2010; Mu, Li & Sun, 2010; Miller, Owens & Rorslett, 2011). Colour may have a functional role such as physiological defence through antioxidants (Steyn *et al.*, 2002; Cazzonelli, 2011) or defence from herbivory through crypsis (Klooster, Clark & Culley, 2009). Flower colour may also have a role in the heating of reproductive organs (Mu *et al.*, 2010; Little *et al.*, 2016).

CONCLUSION

Our analyses of the distribution of flower colour and *Bombus* species across the PAF regions found that the abundance of blue-purple flowers was positively correlated to the number of *Bombus* species, as expected given the association of this flower colour with *Bombus* pollination. Further, we found that the proportions of plant species with blue-purple flowers and their abundance, and the number of *Bombus* species, were greatest in areas that were not glaciated during the Pleistocene, suggesting stable environments support the retention and/or evolution of efficient pollination mutualisms. Our results also suggest that pollinator deficiencies have affected the post-glacial (re)colonization efficiency of blue-purple flowers. Tentative pollinator deficiency and less pollinator dependency due to alternative reproduction modes like asexuality and self-pollination may explain the increased abundance of white-coloured flowers, as pigment production without the benefit of pollination to offset the energy cost may reduce fitness under marginal arctic conditions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1.   Generalized Linear Model output assessing species proportions in relation to glaciation.