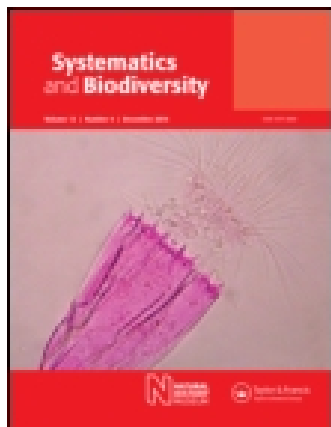


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Bumblebees, climate and glaciers across the Tibetan plateau (Apidae: Bombus Latreille)

Paul H. Williams^{ab}, Nadia Bystrakova^b, Jiaying Huang^a, Zhengying Miao^c & Jiandong An^a

^a Key Laboratory for Insect-Pollinator Biology of the Ministry of Agriculture, Institute of Apiculture, Chinese Academy of Agricultural Sciences, Beijing 100093, China

^b Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

^c Gansu Institute of Apiculture, Tianshui 741022, China

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Research Article

Bumblebees, climate and glaciers across the Tibetan plateau (Apidae: *Bombus* Latreille)

PAUL H. WILLIAMS^{1,2}, NADIA BYSTRIAKOVA², JIAXING HUANG¹, ZHENGYING MIAO³ & JIANDONG AN¹

¹Key Laboratory for Insect-Pollinator Biology of the Ministry of Agriculture, Institute of Apiculture, Chinese Academy of Agricultural Sciences, Beijing 100093, China

²Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

³Gansu Institute of Apiculture, Tianshui 741022, China

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The Tibetan plateau and its immediately surrounding mountains include the greatest hotspot of diversity worldwide for bumblebees, which are among the most important pollinators in temperate ecosystems. We make the first quantitative description of variation in the species composition of alpine social bumblebee faunas across the Tibetan plateau, for 44 species in 124 of the 307 one-degree grid cells. Data were compiled from field surveys, published sources and museum collections. Sampling effort could not be standardized across the region so our inferences have to be provisional. Faunal variation is described using detrended correspondence analysis (DCA); the faunal variation explained by climate variation is described using canonical correlation analysis (CCA); and the contribution of the climate data to the explanation is assessed using Procrustes analysis. Results show: (1) a particularly distinct group of endemic Himalayan faunas in the south; (2) a group of Tibetan interior faunas, with connections to faunas in the north-west in the Hindu Kush, Pamir and Tian Shan; and (3) a group of faunas in north-eastern Qinghai and Gansu, with connections to faunas to the north-east in Mongolia. The eastern and southern faunas in wetter habitats appear to be closer to equilibrium with climate factors, whereas some western faunas in more arid habitats appear further from equilibrium with the measured climate factors. One possibility is that these western faunas may depend on highly localized factors for mitigating the low precipitation over much of this region, and particularly on continuous summer streams with meltwater from distant permanent glaciers or high-ridge precipitation. Consequently, conservation threats to Tibetan bumblebees now include climate change causing loss of permanent streams in the west as well as the over-grazing documented in the east, threats that have not been major concerns for bumblebee conservation elsewhere.

Key words: alpine, biogeography, climate change, equilibrium, grazing, Himalaya, mountain, pollinator, Qinghai, Xizang

Introduction

Bumblebees are among the most important pollinators of both natural and agricultural ecosystems in temperate regions (Goulson, 2010; Velthuis & Doorn, 2006). Their conservation is a concern because some species have declined dramatically, explained hitherto by threats from habitat loss (usually caused by agricultural intensification), pathogens and pesticides (Cameron et al., 2011; Fürst, McMahon, Osborne, Paxton, & Brown, 2014; Whitehorn, O'Connor, Wackers, & Goulson, 2012; Williams & Osborne, 2009). Worldwide the greatest regional hotspot of bumblebee diversity is associated with the Tibetan plateau and the immediately surrounding

mountains (Williams, 1998). Yet despite this richness, the bumblebees of the Tibetan region have received relatively little investigation, taxonomically or ecologically. Most previous work on the region's bumblebees has consisted of simple lists of specimens and species (e.g. Skorikov, 1933a; Wang, 1982; Wang & Yao, 1996) or has sought to compare these lists with those of neighbouring regions within a larger Asian context (e.g. Panfilov, 1957; Skorikov, 1931; Williams, 1996). Here we seek to make an exploratory analysis of variation in the faunal composition at the species level across the Tibetan region and to examine the relationship of this variation to climate.

Several problems have held back the study of Tibetan bumblebees: (i) physical barriers in the form of the highest mountains in the world; (ii) the vast size of the region with few roads; (iii) the physiological challenges of

Correspondence to: Paul Williams. E-mail: paw@nhm.ac.uk; Jiandong An. E-mail: anjiaandong@caas.cn.

working at high elevation; and (iv) political and cultural constraints. Another problem is that bumblebees can be difficult to find because the plateau becomes progressively more sparsely vegetated towards the north and west (Chang, 1981; Wang et al., 2013; Atlas of the Tibetan Plateau in Yu, Luedeling, & Xu, 2010), where suitable habitats become small, distantly isolated patches (Williams, 1991).

Much of what is known of the bumblebee species of the Tibetan region comes from material from the northern plateau collected by 19th century Russian collectors (accounts in Bretschneider, 1981) and described by Russian entomologists (including Morawitz, 1875, 1883, 1887; Radoszkowski, 1860; Skorikov, 1910, 1912, 1914a, 1914b, 1931, 1933b). Similarly, material from the south and east was described by European and American entomologists (including Bingham, 1897; Bischoff, 1936; Cockerell, 1910; Friese, 1905, 1909, 1918; Frison, 1935; Reinig, 1940; Richards, 1928; Smith, 1852, 1871, 1879; Tkalcu, 1968; Vogt, 1908, 1911). This includes the highest records of bumblebees known worldwide (Richards, 1930; Williams, Ito, Matsumura, & Kudo, 2010). In qualitative summaries of these data, comparing the fauna of the Tibetan region with other neighbouring regional faunas, both Skorikov (1931) and Panfilov (1957) proposed that there is a main Tibetan fauna, a Himalayan fauna in the south, and a fauna of Gansu (Skorikov) or Qinghai (Panfilov) in the northeast. Panfilov also suggested an absence of bumblebees from large areas of the central Tibetan plateau and the central Kunlun mountains.

Recently more information on the distribution of Tibetan bumblebees has become available from studies by Chinese biologists, initially from the Chinese Academy of Sciences' Institute of Zoology in Beijing (IZB: Wang, 1979, 1982, 1988; Wang & Yao, 1996). Much of the most recent activity has been coordinated from the Chinese Academy of Agricultural Sciences' Institute of Apiculture in Beijing (IAB: Williams, An, Huang, & Yao, 2010) with the cooperation of other Chinese institutes, including the Gansu Institute of Apiculture in Tianshui and the Tibet Academy of Agricultural and Animal Husbandry Sciences in Lhasa. These surveys have helped to provide many new samples supported with improved information about localities from GPS data (Table 1, e.g. An, Williams, Miao, & Zhou, 2011), as well as a revised taxonomy based on both morphological and molecular evidence (e.g. Williams, An, & Huang, 2011; Williams et al., 2012).

In this paper, we make the first quantitative analysis of variation in faunal composition and examine the relationship of this faunal variation to climate. Because we use disparate data sources, sampling effort could not be standardized across the region and our inferences must be provisional. From the results, we suggest that among the more severe threats to bumblebees in parts of this region is climate change, in particular where it might act through

Table 1. Bumblebee data from states and provinces overlapping the Tibetan plateau from Institute of Apiculture Beijing (IAB) surveys 2007–2012, together with data from the Natural History Museum London (NHM), and from published accounts.

State/province	Number of specimens (all species from all elevations)	Source
Pakistan + Kashmir	6312	Williams, 1991,
Uttarakhand	26	Williams & Cameron, 1993,
Nepal	2762	Williams, Ito, et al., 2010
Xizang	1120 + 281	IAB + NHM
Qinghai	1760 + 220	IAB + Qinghai field surveys (2010–2013)
Yunnan	4752	IAB
Sichuan	6705 + 296	Williams et al., 2009 + IAB
Gansu	5941 + 2261	J.-D. An et al., 2011 + IAB (2011–2013)
Total	32,436	

Data combined subsequently with species-level-only records from the Institute of Zoology Beijing (IZB) published by: S.-F. Wang, 1979, 1982, 1988; S.-F. Wang & Yao, 1996.

the loss of summer streams. We also consider where future sampling should be focused.

Materials and methods

Areas

We are interested in the Tibetan plateau as a habitat for bumblebees. Consequently, we differ from some recent authors who have considered just those parts of the plateau administered by China, typically the Xizang Autonomous Region plus the Province of Qinghai (Mao et al., 2013), or who have included just the adjacent parts of other Chinese provinces (Shen et al., 2014). Instead we define the Tibetan plateau more broadly from structural limits to include parts of China, Nepal, Bhutan, India and Pakistan, in a region that is bounded to the north by the Tarim Basin and Hexi Corridor, to the east by the Sichuan basin, and to the south by the foothills and lowlands of Yunnan, India and Pakistan. To the west, we choose a limit at the Wakhan and Taxkurgan valleys, which is near the western distribution limit of characteristic Tibetan bumblebee species (Williams, 1991) such as *Bombus rufofasciatus* (Fig. 1: the gap in the west Himalayan distribution is almost certainly from lack of sampling).

The Tibetan plateau is more deeply divided by valleys in the wetter east (Tsangpo, headwaters of the Salween, Mekong, Yangtze etc.: Chang, 1981; Korup & Montgomery, 2008). Here, forests extend further into the plateau along the valleys (Atlas of the Tibetan Plateau in Yu et al., 2010), where they are accompanied by a forest fauna of bumblebees (Wang, 1982, 1988; Williams, Tang, Yao, &

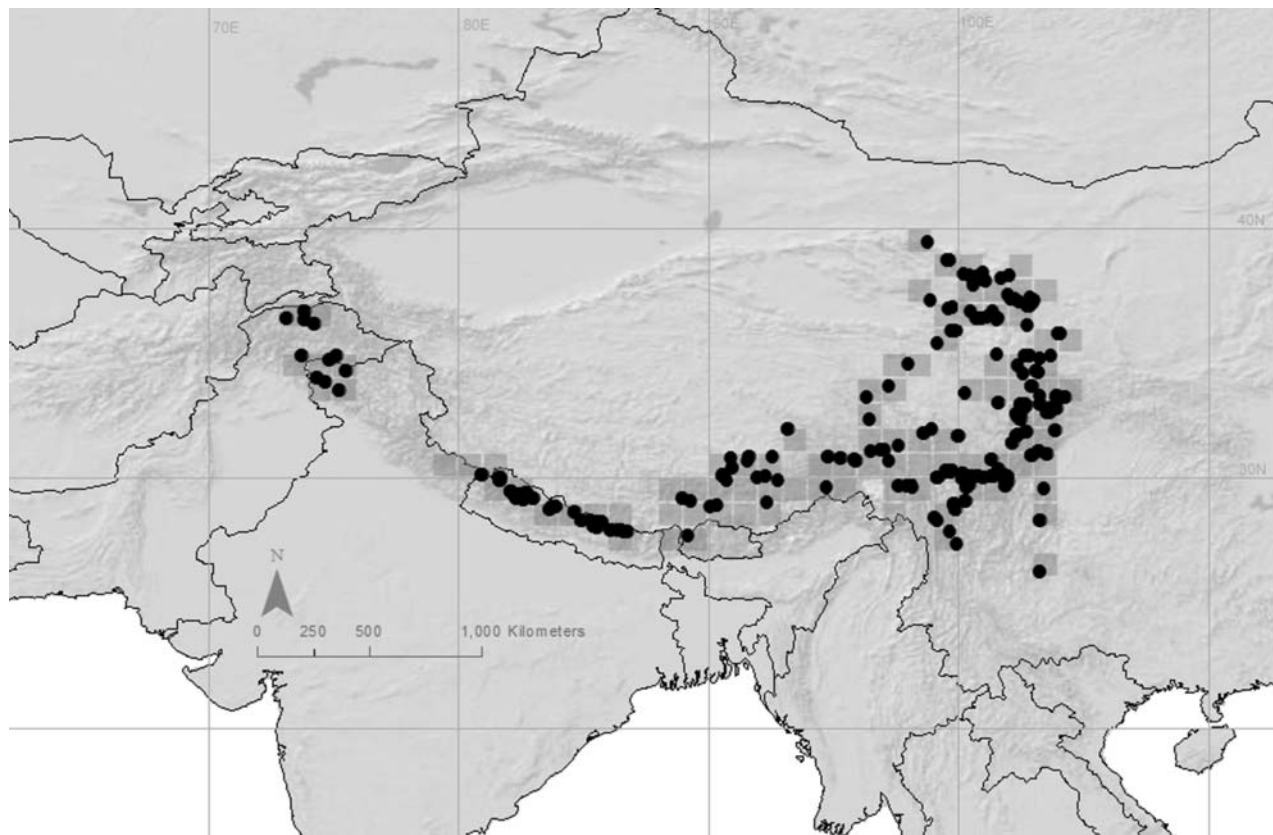


Fig. 1. Relief map with hill shading for the region centred on Tibet with (black lines) borders to national administration as in UN maps, and showing the global range of *Bombus rufofasciatus* as known from (black spots) point records from the IAB and NHM collections and as (grey squares) cells on a $1^\circ \times 1^\circ$ grid from all data in Table 1.

Cameron, 2009). We have attempted to exclude the southeastern forest fauna of bumblebees and to limit our analyses to the faunas of the alpine zone that are more broadly comparable across the plateau. The upper limits of the montane forest zone below and of its bumblebee fauna are variable in different locations and with different aspects, so we adopt an approximate upper elevation threshold for this zone of 3000 m a.s.l., based on studies of bumblebees in Kashmir in the west (Williams, 1991) and of Sichuan in the east (Williams *et al.*, 2009). We have not needed to define an upper limit to this zone (the 'snow line') because there is no bumblebee fauna above it. The land above 3000 m elevation defines the study area shown in grey in Fig. 2, which is just less than 3.8 million km² (approximately one third of the size of the USA or Europe). We refer to this region (which extends beyond China) as the Qinghai-Tibetan plateau in our broad sense (henceforth QTP).

We are interested in broader regional rather than more local patterns in faunal variation, so we agglomerate site data into $1^\circ \times 1^\circ$ grid cells to approximate regional species pools. At this scale and for bumblebees as social, central-place foragers (tied to colonies), it is likely that few bumblebee records represent vagrant individuals. These

grid cells measure *c.* 110×90 km within this region and therefore are of nearly equal-area extent. The number of species in an area depends strongly on the extent of the area (Connor & McCoy, 1979), so statistics for equal-area grid cells have the advantage of being more directly comparable. This avoids the severe bias that is inherent when comparing administrative units of very different extent (cf. Mao *et al.*, 2013). We are unable to adjust grid-cell species-richness scores (or other derived faunal scores) for differences in sample sizes among cells by applying random re-sampling of records to a standard sample size (Biesmeijer *et al.*, 2006; Colwell *et al.*, 2012; Gotelli & Colwell, 2001; Heck, Belle, & Simberloff, 1975; Williams, 2000) because some of our data sources do not record numbers of individuals per species (Table 1 footnote). This re-sampling is also incompatible with multi-variate analysis because it removes species' identities. We therefore treat the data for this preliminary analysis as though species' distributions were completely known, even though this is unlikely to be the case (e.g. the gaps in Fig. 1). Consequently our inferences have to be provisional until better survey data are available.

Older surveys of parts of the QTP are documented with bumblebee distribution data by Wang (1982, 1988) and

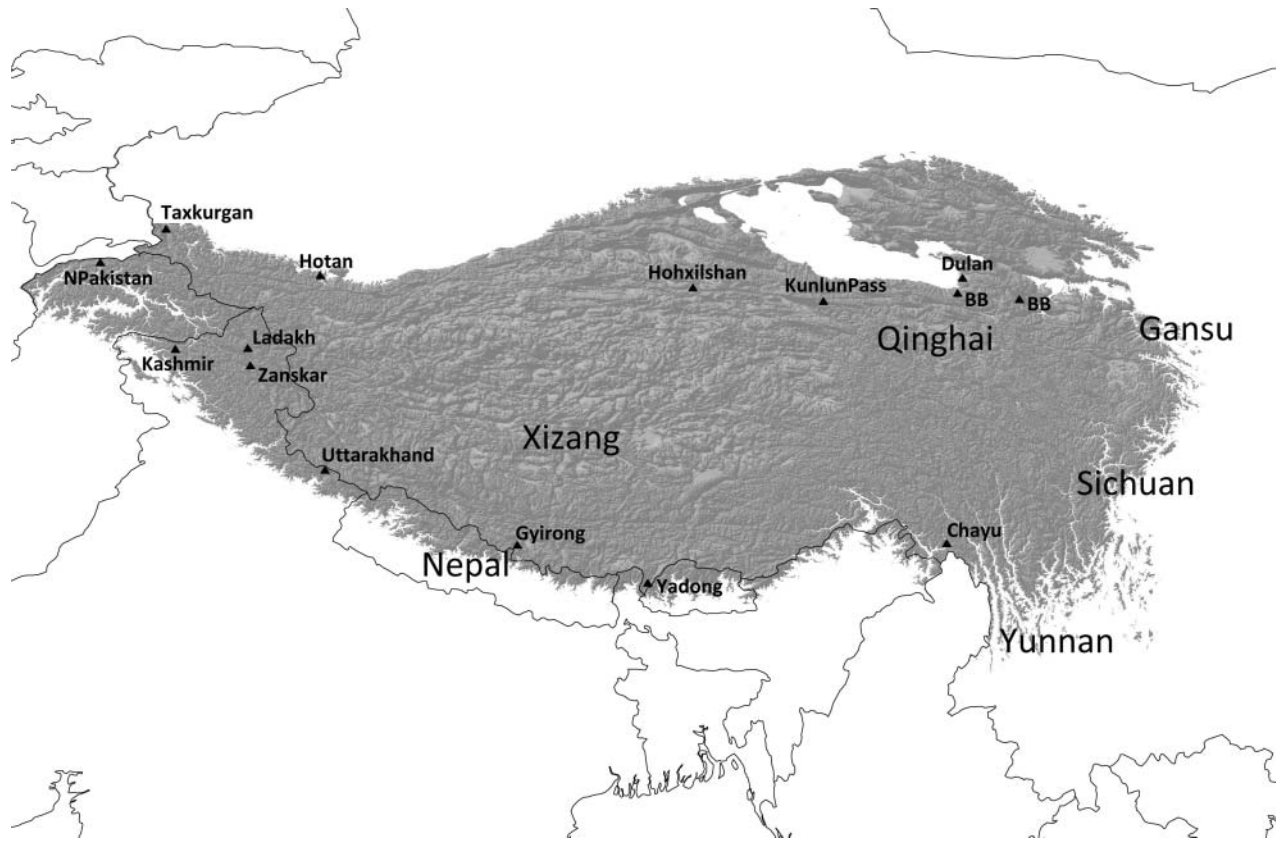


Fig. 2. Map showing (in grey) the region of the Tibetan plateau above 3000 m (QTP in our broad sense) that is considered for analysis, with (black lines) borders to national administration as in Fig. 1. Selected countries, provinces and sample sites are labelled (BB, Burhan Budai mountains).

by Wang and Yao (1996). More recent surveys have been made of Pakistan, Kashmir, Nepal, Xizang, Qinghai, Yunnan, Sichuan and Gansu (Table 1). In addition, the authors JH, PW and ZM have conducted fieldwork during surveys across Qinghai in 2010–2013. Records from Tkalců (1961) are duplicated in the more recent surveys with GPS data.

Species

We have applied filters to the species recorded in the surveys from Table 1 to: (i) include only non-parasitic species (i.e. exclude species of the subgenus *Psithyrus* Lepeletier) with comparable social ecology; (ii) include only records from sites above 3000 m (from GPS/GoogleEarth data) to restrict data to the alpine zone; and (iii) include only species with mean elevations of records above 3000 m, to restrict data to the alpine specialist species (from data in An et al., 2014; Williams, 1991; Williams, Ito, et al., 2010; Williams et al., 2009; IAB, IZB, NHM collections). One of the challenges in studying bumblebees is that species are often variable in colour pattern (Williams, 2007), so that there are often many synonyms per species (Williams, 1998). The larger

taxonomic framework follows a synoptic and well-supported study of five genes (Cameron, Hines, & Williams, 2007; Williams, Cameron, Hines, Cederberg, & Rasmont, 2008), but closely related taxa are assessed using phylogenetic analysis of the faster-evolving COI barcodes (An et al., 2014; Williams et al., 2011; Williams et al., 2012; Williams, Ito, et al., 2010). Two species (*B. kashmirensis*, *B. ladakhensis*) are each split into two taxa that have been regarded previously as separate species (Wang, 1982; Wang & Yao, 1996) or as regionally endemic subspecies segregated within the QTP (Richards, 1928, 1930). These are recognized by yellow-banded colour patterns in the west (*meinertzhageni* and *ladakhensis* respectively) and by white-banded colour patterns in the east (*kashmirensis* and *phariensis* respectively). All species identifications in the references in the body of Table 1 were made by one of us (PW) for consistency. Relevant specimens in the IZB collection (Table 1 footnote) have also been sorted and checked. The compiled presence/absence data file is available from PW.

Bumblebee species of the QTP can be classified by their broader distributions depending on where they extend into external regions. There are no bumblebees to the south in lowland India (Williams, 1991) and few alpine species

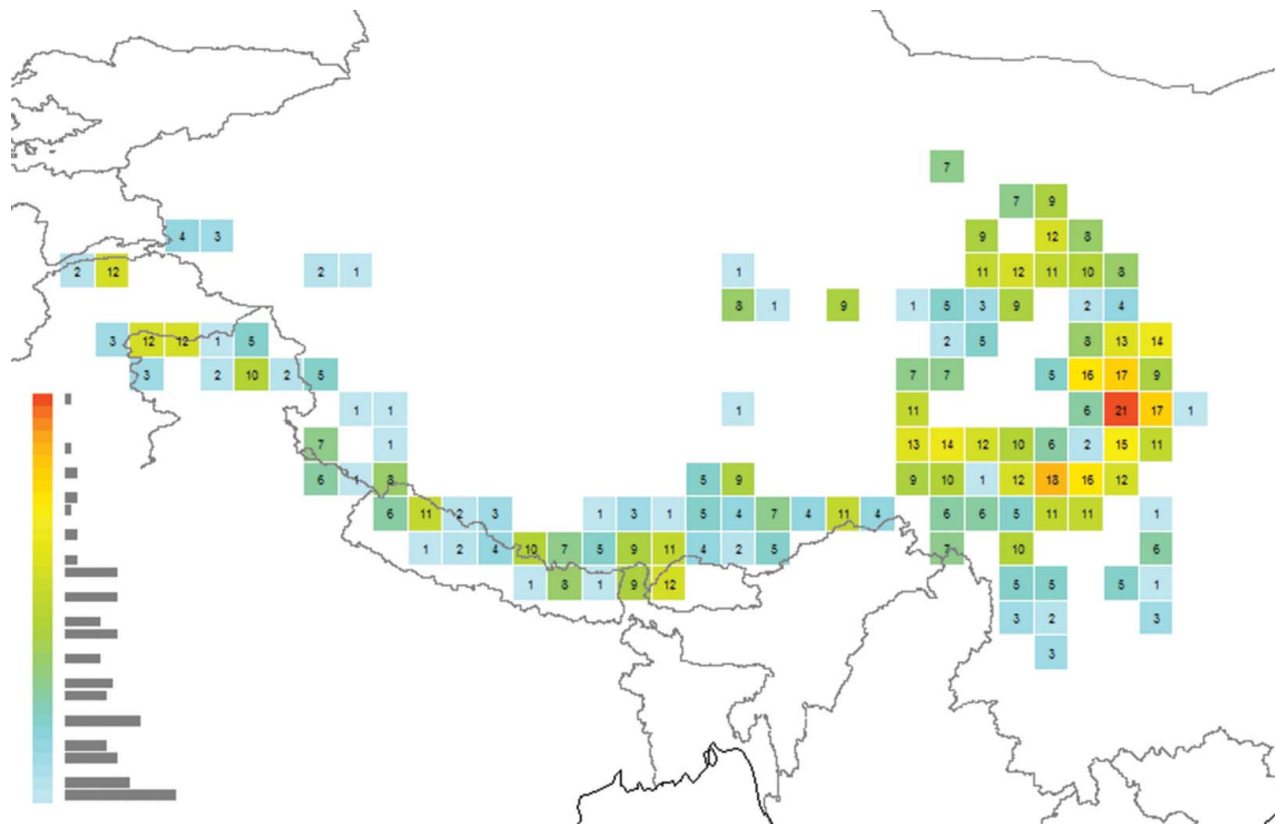


Fig. 3. Numbers of social bumblebee species of the alpine zone recorded per QTP $1^\circ \times 1^\circ$ grid cell (124 recorded grid cells) from data after applying the three filters (see the text), with an equal-interval colour scale (left) and a histogram showing the frequencies of grid cells in each colour class.

occur to the east at lower elevations in North China (e.g. in Ningxia, Shaanxi, Shanxi, etc.: An *et al.*, 2014). Consequently, species may be endemic to the QTP and the immediately adjacent mountains; or they may also occur to the west and north of the QTP in the Hindu Kush, Pamir and Tian Shan mountains (*cf.* Reinig, 1930; Skorikov, 1931; Tkalců, 1969; Williams, 2011); or they may also occur to the east and north of the QTP in some of the Mongolian mountains, such as in the Altai (*cf.* Tkalců, 1974).

Many QTP grid cells have low recorded species richness, as shown by the skewed histogram of score frequencies against the colour scale in Fig. 3. In some grid cells, especially in the north and west, there may be genuinely just one or two species present (e.g. parts of the Indus Valley, Williams, 1991), although from field observations this is less likely to be genuine in the south and east (see the discussion). For analysis of faunal composition, we apply another filter to remove most grid cells with recorded richness below 5 species (the lowest 19% of richness scores), because these grid cells are expected to be the most severely under-recorded, at least in the south and east of the region. Exceptions are made for two of the four grid cells in the far north-west, where faunas in these extreme environments may genuinely be smaller.

Climate variables

We suggest some of the climate variables that are most likely to govern the reproductive success of bumblebee colonies in the QTP in Table 2. From an analysis of inter-correlations (see Appendix Fig. S1, online supplemental material, which is available from the article's Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2014.982228>), we include for the analysis of climatic variation only variables that are more nearly independent of one another and less strongly correlated with others: mean temperature of the warmest quarter (highly correlated with maximum temperature of the warmest month, but with slightly lower correlation with water deficit), precipitation of the wettest month (highly correlated with precipitation of the warmest quarter, but with slightly lower correlation with days of rain), ratio of precipitation of the wettest month to precipitation of the warmest quarter, growing degree days above $+5^\circ\text{C}$, water deficit, irradiance in the warmest quarter, and days of rain (all correlations < 0.75). Contributions of climate variables to the bumblebee canonical correspondence analysis (CCA) model were assessed using permutation tests. Both forward and reverse permutation tests showed that the contribution

Table 2. Climate variables proposed here as most likely to affect bumblebee-colony reproductive success.

Variable	Acronym	Units	Source	Resolution	Proposed mechanism
Max temperature of the warmest month	mxTwm	°C	BIOCLIM: BIO5 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005)	30 arc sec (c. 1 km)	Extreme values reduce food-plant nectar and pollen production and also profitable foraging opportunities
Mean temperature of warmest quarter	mnTwq	°C	BIOCLIM: BIO10 (Hijmans et al., 2005)	30 arc sec (c. 1 km)	Extreme values reduce food-plant nectar and pollen production and also profitable foraging opportunities
Irradiance in the warmest quarter	irrwwq	W/m ²	CliMond: BIO26 (Kriticos et al., 2012)	10 arc min (c. 20 km)	Extreme values reduce food-plant nectar and pollen production
Growing degree days, above threshold of +5° C	gdd5	days	Atlas of the Biosphere (sage.wisc.edu/atlas) (New, Hulme, & Jones, 1999)	30 arc min (c. 50 km)	Low values reduce food-plant nectar and pollen production, reduce profitable foraging opportunities, and reduce the seasonal window for colony development
Precipitation in the wettest month	pptwm	mm	BIOCLIM: BIO13 (Hijmans et al., 2005)	30 arc sec (c. 1 km)	High values (if in the summer as here) reduce foraging opportunities
Precipitation in the warmest quarter	pptwq	mm	BIOCLIM: BIO18 (Hijmans et al., 2005)	30 arc sec (c. 1 km)	Low values reduce food-plant nectar and pollen production, and high values reduce foraging opportunities
Ratio: precipitation in the wettest month to precipitation in the warmest quarter	pptm/q	—	Calculated from BIOCLIM: BIO13/BIO18 (Hijmans et al., 2005)	30 arc sec (c. 1 km)	High values for a relatively intense month of rainfall (if from wet summer months as here) reduce foraging opportunities
Number of days of rain in the warmest quarter	ndrwq	days	CGIAR: DaysOfRain (ccaifs-climate.org/)	5 arc min (c. 10 km)	High values reduce foraging opportunities
Water deficit	wdef	mm/day	CGIAR: PET-AET (cgair-csi.org/data)	30 arc sec (c. 1 km)	High values reduce food-plant nectar and pollen production

of GDD to the CCA model was not significant, so this variable can be presumed redundant and excluded. Therefore the final CCA model includes six variables: ratio of precipitation of the wettest month to precipitation of the warmest quarter, water deficit, irradiance in the warmest quarter, and days of rain, precipitation in the wettest month, and mean temperature of the warmest quarter.

Analytical techniques

We explore variation in bumblebee faunal composition using detrended correspondence analysis (DCA: as implemented in DECORANA, Hill, 2012). The degree to which variation in the species composition of bumblebee faunas is explained by variation in climate among areas is explored using canonical correspondence analysis (CCA: Legendre & Legendre, 1998; implemented in the Vegan package in R 3.0.2, r-project.org, accessed 2013). To quantify how much of the faunal variation is explained by climatic variation at different sites, we compare results from the CCA analysis when constrained and unconstrained (CA) by the climate data, using a Procrustes superimposition (Peres-Nato & Jackson, 2001). This quantifies the mismatches between the CA/CCA as residuals and minimizes the sum-of-squares of these residuals.

Results

Variation in species richness

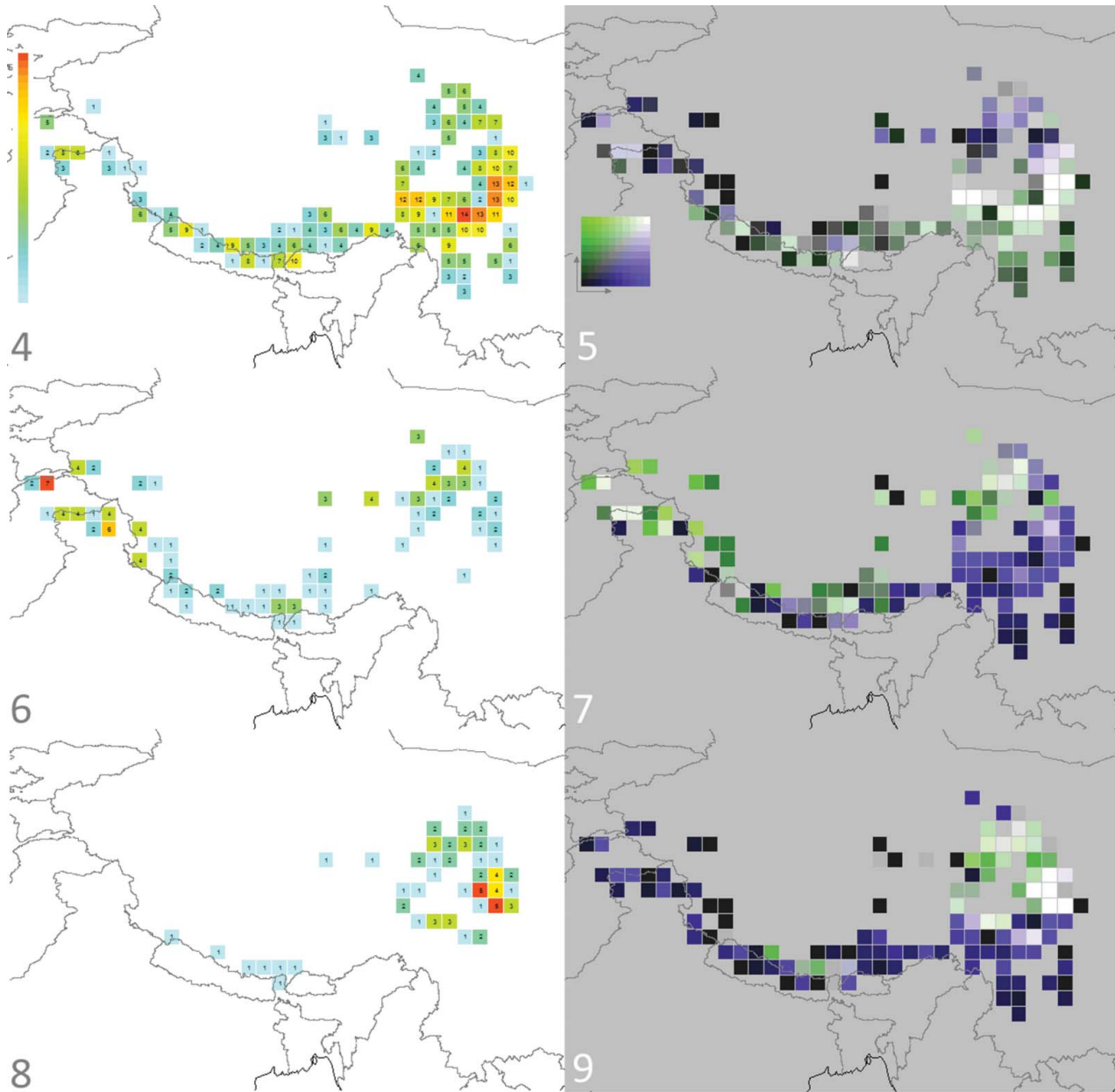
There are 82 bumblebee species known from the provinces (Table 1). After applying our first three filters for social bumblebee species of the QTP alpine zone (the grey region of Fig. 2), we retain 44 species in Table 3 (this Table includes the authors for all included bumblebee taxon names). This list of species seeks to resolve synonyms and misidentifications among the taxa named in the studies (Table 1). Figure 3 shows that there are more of these species per grid cell in the east than in the west of the QTP. There are fewer cells with records in the northern and central interior regions.

Variation in faunal composition

More than half of the alpine QTP bumblebee species are endemic to the QTP (Table 2: 26/44 = 59%). Figure 4 shows that the endemic species are concentrated (Fig. 4: orange) in the east of the QTP, where there are no closely neighbouring high mountains beyond the plateau. There is disproportionately high endemism (Fig. 5: green) in the fringing mountains of the south (i.e. this endemic fauna is essentially a Himalayan fauna), with relatively fewer

Table 3. Social bumblebee species of the alpine/subalpine zone of the Tibetan plateau, with external distribution ranges: E, endemic; W, north-western; N, north-eastern species.

Subgenus	Species	Synonyms in the principal data sources	Range
<i>Mendacibombus</i>	<i>superbus</i> (Tkalčů)		E
	<i>waltoni</i> Cockerell		E
	<i>convexus</i> Wang		E
	<i>turkestanicus</i> Skorikov		W
	<i>himalayanus</i> (Skorikov)		E
	<i>marussinus</i> Skorikov		W
	<i>avinoviellus</i> (Skorikov)		E
<i>Subterraneobombus</i>	<i>margreiteri</i> Skorikov		N
	<i>personatus</i> Smith		E
	<i>melanurus</i> Lepeletier		W
	<i>difficillimus</i> Skorikov	<i>difficillimus</i> [sic] (Wang, 1982; Wang & Yao, 1996), <i>melanurus</i> s. l. (Williams, 1991 in part)	W
<i>Megabombus</i>	<i>supremus</i> Morawitz		E
	<i>sushkini</i> (Skorikov) s. l.		N
<i>Thoracobombus</i>	<i>laesus</i> Morawitz s. l.		N
	<i>filchnerae</i> Vogt		N
	<i>humilis</i> Illiger		N
<i>Pyrobombus</i>	<i>impetuosus</i> Smith s. l.	<i>yunnanensis</i> [sic] (Wang, 1982, 1988)	E
	<i>subtypicus</i> (Skorikov)		W
	<i>abnormis</i> (Tkalčů)		E
	<i>mirus</i> (Tkalčů)		E
	<i>lemniscatus</i> Skorikov		E
	<i>lepidus</i> Skorikov	<i>yunnanicola</i> [sic] (Wang, 1982)	E
	<i>infirmus</i> (Tkalčů)		E
	<i>pressus</i> (Frison)		E
	<i>biroi</i> Vogt		W
	<i>kotzschii</i> Reinig	<i>biroi</i> s. l. (Williams, 1991 in part)	W
	<i>wangae</i> Williams <i>et al.</i>		E
<i>Bombus</i> s. str.	<i>longipennis</i> Friese	<i>lucorum</i> s. l. (Wang, 1982, 1988; Williams, 1991 in part; Wang & Yao, 1996; Williams <i>et al.</i> , 2009, 2010; An <i>et al.</i> , 2011)	E
	<i>minshanensis</i> Bischoff	<i>patagiatus</i> s. l. (Wang, 1982; Williams <i>et al.</i> , 2009; An <i>et al.</i> , 2011 in part)	E
<i>Alpigenobombus</i>	<i>kashmirensis</i> Friese	<i>meinertzhageni</i> , <i>tetrachromus</i> (Wang, 1982; Wang & Yao, 1996)	E
	<i>nobilis</i> Friese	<i>chayaensis</i> (Wang, 1982)	E
	<i>validus</i> Friese	<i>nobilis</i> s. l. (Williams <i>et al.</i> , 2009 in part; An <i>et al.</i> , 2011 in part), <i>xizangensis</i> (Wang, 1982, 1988)	E
<i>Melanobombus</i>	<i>miniatus</i> Bingham	<i>eurythorax</i> , <i>stenothorax</i> (Wang, 1982), <i>pyrosoma</i> s. l. (Williams, 1991)	E
	<i>richardsiellus</i> (Tkalčů)		E
	<i>rufofasciatus</i> Smith		E
	<i>friseanus</i> Skorikov	<i>richardsi</i> (Wang, 1982)	E
	<i>tanguticus</i> Morawitz		E
	<i>ladakhensis</i> Richards	<i>phariensis</i> (Wang, 1982; Wang & Yao, 1996)	E
	<i>keriensis</i> Morawitz	<i>niveatus</i> , <i>tenellus</i> , <i>trilineatus</i> (Wang, 1982; Wang & Yao, 1996), <i>incertus</i> (Wang & Yao, 1996)	W
	<i>semenovianus</i> (Skorikov)		W
	<i>sichelii</i> Radoszkowski		N
	<i>oberti</i> Morawitz	<i>xionglaris</i> , <i>duanjiaoris</i> , <i>zhadaensis</i> (Wang, 1982)	W
<i>Sibiricobombus</i>	<i>sibiricus</i> (Fabricius)	<i>flaviventris</i> (Wang, 1982; Wang & Yao, 1996)	N
	<i>asiaticus</i> Morawitz	<i>heicens</i> , <i>huangcens</i> , <i>miniatocaudatus</i> (Wang, 1982), <i>miniatpcaudatus</i> [sic] (Wang & Yao, 1996)	W



Figs. 4–9. Figs. 4, 6, 8: absolute numbers of selected social bumblebee species of the alpine zone from Table 3 recorded per QTP $1^\circ \times 1^\circ$ grid cell, with an equal-interval colour scale (left). Figs. 5, 7, 9: relative numbers of selected species from Figs 4, 6, 8 (in green) compared with the numbers of all species from Fig. 3 (in blue) recorded per $1^\circ \times 1^\circ$ grid cell (124 recorded grid cells), using an equal-frequency two-colour scale (this is shown on the left of Fig. 5: mutual low richness scores are shown in black, mutual high scores in white, covarying intermediate scores in grey; increasing relative total richness appears as an increasing saturation of blue and increasing relative selected richness appears as an increasing saturation of green, as in Williams & Gaston, 1998). In Figs 4, 5 the selected species are endemic species; in Figs 6, 7 the selected species are western species; and in Figs 8, 9 the selected species are north-eastern species (as listed in Table 3).

endemics in the north and interior (Fig. 5: blue). In contrast, Figs 6–7 show that the north and interior have a disproportionate (Fig. 7: green) richness of the western species from the Hindu Kush, Pamir and Tian Shan that extend eastwards into the QTP. Many of these western species (Fig. 7: green) reach through the Kunlun mountains into the Burhan Budai mountains (Fig. 2) of the

northeastern QTP. Figures 8–9 show the species shared with areas beyond the QTP to the north and east, in the Mongolian mountains. Unsurprisingly, these species are relatively rich in the north-eastern corner of the QTP (Fig. 9: green), with only *B. sibiricus* among them spreading further west into the southern interior, to the north of Nepal.



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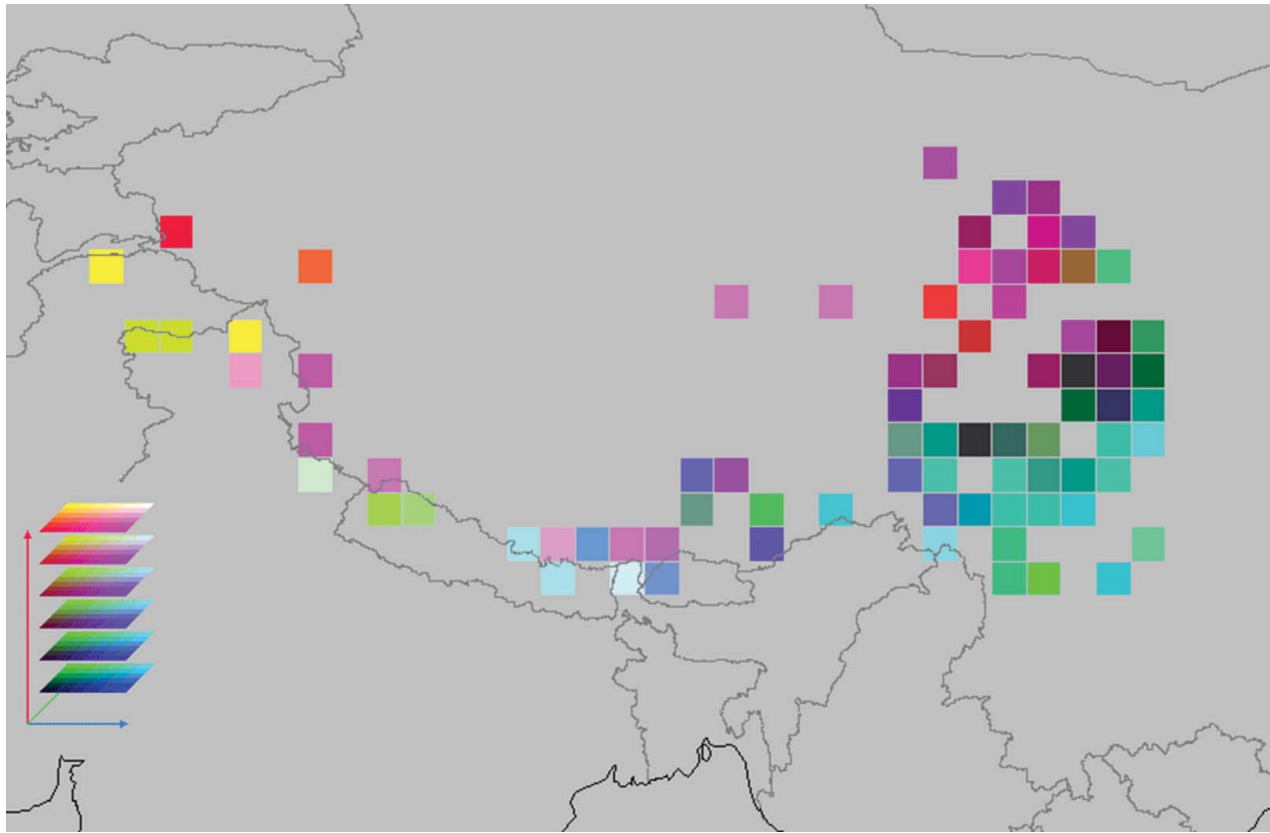


Fig. 11. Plotting DCA scores for the 80 included QTP bumblebee faunas (Fig. 10) on axes 1–3 in intensities of red (DCA1), green (DCA2), and blue (DCA3, see the colour scale left), using equal-frequency colour classes (Williams, de Klerk, & Crowe, 1999). DCA1 shows north-west to south-east variation between high scores (left-red) for Central Asian faunas to low scores (right) for Central China faunas. DCA2 shows south to north variation between high scores (bottom-green) for Himalayan fringe faunas to low scores (top) for northern interior faunas. DCA3 shows central to east/west variation between high scores (centre-blue) for central faunas to low scores (sides) for eastern and western faunas.

B. difficillimus, *B. keriensis* and *B. melanurus* (these faunas are closely related to the Tibetan interior faunas, of which they are an impoverished subset).

Faunal variation explained by climate

Relationships between climate and faunal variation are shown in Fig. 12 in the climatically constrained CCA space (eigenvalues for the first three CCA axes: 0.45, 0.22, 0.16). Axis 1 (CCA1, Fig. 12) is most positively associated with irradiance and most negatively with days of rain within the summer season of bumblebee activity. The distinctive western grid-cell faunas of Ladakh, North Pakistan, Zaskar, Taxkurgan and Hotan, as well as the northern faunas of the Kunlun mountains (as grouped together in the DCA, Fig. 10), are therefore associated with high summer sunshine and low precipitation. In contrast, the eastern grid-cell faunas (especially Sichuan and Yunnan) are associated with high summer cloud cover and high precipitation. Axis 2 (CCA2, Fig. 12) is most positively associated with the ratio of precipitation in the

wettest month (in the summer, in this area) to precipitation in the warmest quarter (showing a sharp peak of summer precipitation, the monsoon) and most negatively with summer water deficit (drought stress). The distinctive grid-cell faunas of the northern and western mountains (Kunlun, Taxkurgan, Hotan, Zaskar, parts of Qinghai) are therefore associated with arid areas that do not have a strong summer monsoon, although the low precipitation is still highest in the summer. In contrast, the southern grid-cell faunas of the Himalaya (Kashmir, Uttarakhand, Nepal) are associated with a sharp peak of summer monsoon and low water stress.

The effect of including the climate variables, measured as the divergence between the CA and CCA results, is significant (symmetric Procrustes rotation correlation 0.94, permutation test sum of squares 0.113, $P = 0.001$). Figure 13 uses grey lines to represent the residuals between the purely faunal (CA) ordination and the faunal ordination explained by climate (CCA, with triangles). This shows that climate residuals are small for bumblebee faunas in eastern grid cells (corresponding to areas marked with X, Q, G, S on the right of Fig. 12), so that

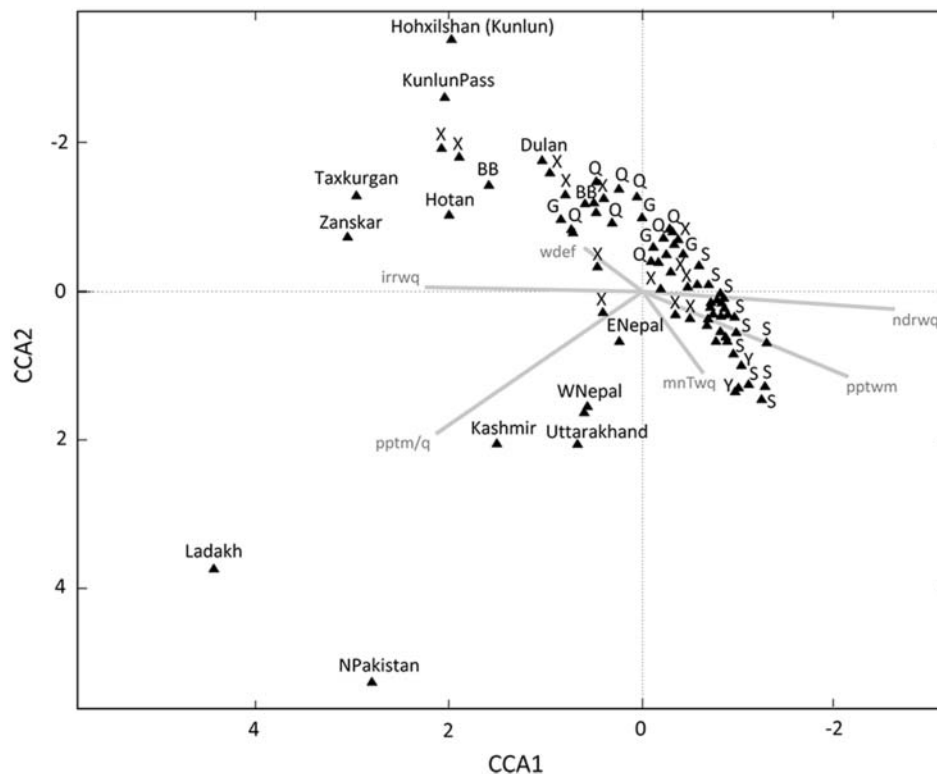


Fig. 12. CCA axes 1 and 2 summarizing variation in composition among the 80 included QTP bumblebee faunas (triangles) constrained by their relationship to the six selected climatic variables (grey). The scales on both axes are reversed in this plot, which preserves in the figure the approximate relative arrangement of the sites from geographic space; abbreviations: BB, Burhan Budai mountains; G, Gansu; Q, Qinghai; S, Sichuan; X, Xizang; Y, Yunnan; wdef, water deficit; irrwq, irradiance in the warmest quarter; pptm/q, ratio of precipitation in the wettest (summer) month to precipitation in the warmest quarter; ndrww, number of days of rain in the warmest quarter; pptwm, precipitation in the wettest month; mnTwq, mean temperature of the warmest quarter.

faunal composition in the east appears generally to be well explained by climate. In contrast, some western grid-cell faunas (on the left of Figs 12–13) such as in Ladakh, have large climate residuals, indicating that in these cases the climate variables are not providing a good explanation of the faunal variation.

Although the largest residuals (Fig. 13) are for grid cells at the western end of CCA1 (Ladakh, Taxkurgan, Hotan, North Pakistan, Kunlun, to the left of Fig. 12), with less frequent (low days of rain) lower rainfall (low precipitation of the wettest [summer] month) and more sunshine (high irradiance in the warmest quarter), nonetheless the high residuals are actually greatest in their displacements along the second CCA axis (the grey lines are orientated more nearly vertically in Fig. 13). Therefore the largest residuals show strong mismatches in the length of the monsoon (which becomes shorter in the southwest, Fig. 12: reflected in the ratio of precipitation of the wettest month to precipitation of the warmest quarter) and in the severity of the water deficit (which increases in the northwest, Fig. 12: water deficit). Thus the largest residuals appear to relate at least in part to the measured water availability in the most arid areas.

Discussion

Species richness

The richness of social bumblebee species in the alpine zone of the QTP region (Table 3: 44 species) is greater than in any other alpine region of the world. The entire bumblebee fauna of all zones of South America is only 24 species (Williams, 1998). Even the total bumblebee fauna of the whole of the USA and Canada across all zones consists of just 40 social bumblebee species (Williams, Thorp, Richardson, & Colla, 2014), but in more than five times the area (19.8 million km², Anonymous, 2001) of the QTP. In Europe, where regional species richness tends to be higher (Williams, 1998: 99 map), Rasmont (1988: 123, 137) identified just seven social bumblebee species in the alpine zone of the Pyrenees, with just one additional species in the Alps. There are no indigenous bumblebees in sub-Saharan Africa or Australia. The high alpine species richness of the QTP is perhaps unsurprising, because bumblebees are most diverse and abundant in mountain regions globally (Williams, 1998) and the QTP consists of a particularly large high-elevation region. Unlike other social bees, not

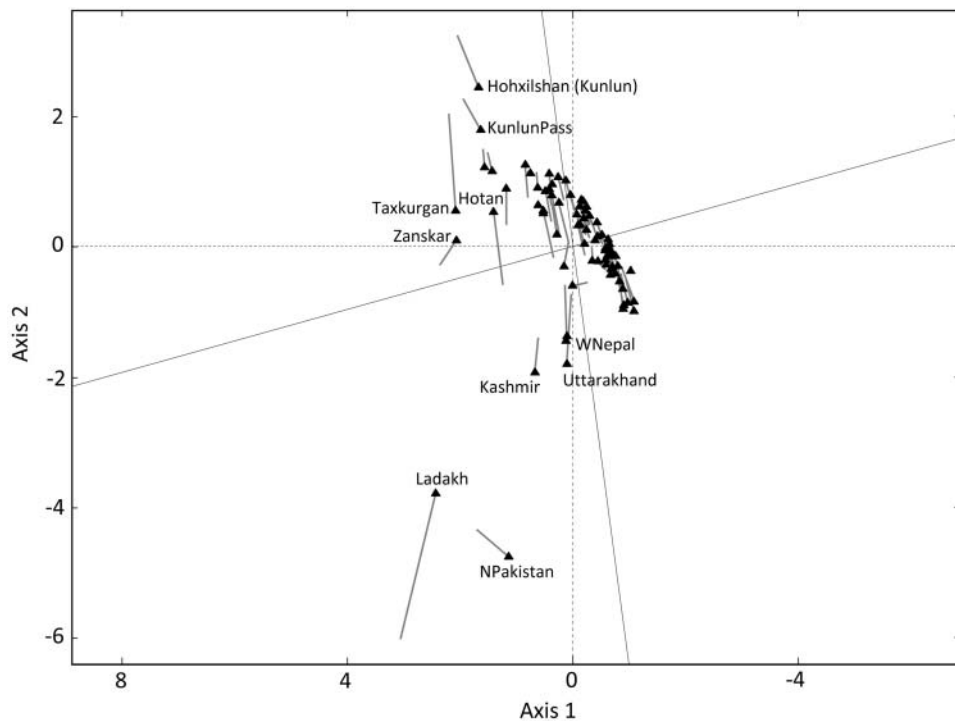


Fig. 13. Plot of faunal samples showing the Procrustes superimposition between unconstrained CA to climatically constrained CCA (triangles) scores and the residuals between them (grey lines). The scale on axis 1 is reversed in this plot, which preserves in the figure the approximate relative arrangement of the sites from geographic space.

only does more effective facultative endothermy enable bumblebees to be active at the lower temperatures of high elevations, but bumblebees can also hibernate (Heinrich, 1979). This substantially reduces energy costs during the predictable long annual season of extreme adverse climate at high elevations.

Species composition

With many new data for QTP bumblebees, our results (Figs 4–9) provide new quantitative evidence that supports Skorikov (1931: his Fig. 10) and Panfilov (1957: his Fig. 3) in recognizing three principal groups of QTP faunas by their species composition. The Himalayan fauna in the south is especially distinctive (Fig. 10), with many endemic species (Figs 4–5, Table 3). These species have their closest relatives to the east in the Oriental region (Williams, 1991: in central and southern China, and south-east Asia). The species of these northern faunas are primarily Palearctic (Williams, 1991, 1996: with broad distributions north of the Chinese arid belt). The new data allow us to begin to map the regions and their intervening transition zones within the QTP with increased spatial resolution (Fig. 11), but better data will be needed to give a clearer picture.

Climatic explanations

A serious problem for surveys in more arid environments is the difficulty of detecting species at low densities and

when patchily distributed across arid terrain (Williams, 1991). Another consequence of this patchiness is that associations between QTP bumblebee faunas and climate in our analysis are likely to be weakened by the inevitably low precision in the match between sparse sampling points for bumblebees and the coarsely interpolated climate-variable surfaces. This mismatch is expected to have an especially strong effect because there is such a high relief in parts of the QTP region.

The principal variation in climatic associations of bumblebee faunas (CCA, Fig. 12) is between the arid west and north of the QTP, on the one hand, and the wetter east and south of the QTP, on the other. This broad pattern is familiar from the vegetation (Chang, 1981; Atlas of the Tibetan Plateau in Yu et al., 2010: their fig. 1; Wang et al., in press) as well as from variation in species richness within different plant groups (Mao et al., 2013). The severe aridification of the west and north of the QTP is believed to be ancient and to be associated with the Tibetan uplift (An, Kutzbach, Prell, & Porter, 2001; Dupont-Nivet et al., 2007; Miao, Herrman, Wu, Yan, & Yang, 2012). This aridification may have imposed a strong filter on bumblebee faunal composition, extirpating susceptible species from some areas, except where local mitigating factors might have left patches with persistent relic faunas. On the other hand, the aridification may have pre-dated the divergence of some of the more recent bumblebee species

and might now be preventing some species in adjacent areas from colonizing the QTP.

Conservation concerns

Not all QTP bumblebee faunas appear equally close to equilibrium with climate in our Procrustes results. The superimposition of CA and CCA results in Fig. 13 shows that faunas are well explained by and therefore apparently closer to equilibrium with our chosen climatic variables in the wetter, eastern QTP (right of Fig. 13), whereas there appears to be greater disequilibrium (higher residuals) in the more arid, western QTP (left of Fig. 13). Nonetheless, the situation appears broadly stable in the west even in the extreme case of Ladakh, where the fauna has remained unchanged since the 1920s (Richards, 1928; Williams, 1991). It is possible that the measured aridity in the west and north of the QTP is actually mitigated for the bees by local, unmeasured factors, and that these factors might be identified from local field observations. Fieldwork has shown that in western and northern areas (in Ladakh, Zaskar, parts of Qinghai) bumblebees are much more restricted to small isolated patches of vegetation with suitable food plants (equivalent to oases, sometimes very sharply circumscribed) surrounded by large, unoccupied and often very sparsely vegetated arid areas, where no food plants have been detected (Williams, 1991: see Appendix Fig. S2 online supplemental material, which is available from the article's Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2014.982228>); and from fieldwork around the Kunlun Pass in 2013). These small western and northern 'oases' appear to be strongly dependent on narrowly localized irrigation by continuous summer streams (for which we have no data), rather than on widespread direct summer precipitation as they are in the wetter east, in parts of Qinghai, Gansu, Sichuan and Yunnan (An *et al.*, 2011; Williams *et al.*, 2009: see Appendix Fig. S3, online supplemental material, which is available from the article's Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2014.982228>). In the west and north, the continuous summer streams are often fed by meltwater from permanent glaciers, although summer precipitation also appears (from fieldwork and from satellite images) to be more narrowly confined to the high mountain ridges, from where it might contribute to the same streams. Continuous summer streams in the west and north could provide local relief to the bumblebees' food plants from the regional pattern of high drought stress in otherwise arid areas, so that beside these streams, food plants could produce the nectar and pollen required by bumblebees. However, this effect is expected to be at too fine a scale for it to show up in the (low resolution) climate data used here. The resulting mismatch between measured and effective water availability is proposed as

one possible explanation for some of the larger climate residuals in the Procrustes results (Fig. 13). As a next step we need more field studies to determine whether continuous summer streams in the west and north are indeed an important limiting factor for supporting relictual populations of some bumblebee species.

The QTP has experienced a distinct warming trend in recent decades, associated in its central and southwestern regions with aridification and reduction of grassland growth (Zhang *et al.*, 2013). Some QTP glaciers are now believed to be melting rapidly with climate change (Gardner *et al.*, 2013; IPCC, 2014; Kääb, Berthier, Nuth, Gardelle, & Arnaud, 2012; Qiu, 2008; Xu *et al.*, 2009), although less so in the north and centre of the QTP (Gardner *et al.*, 2013). This is a potential conservation concern, because bumblebees could be especially susceptible to local extirpation or even complete extinction by climatic change if these continuous summer streams were to be lost from the arid west of the QTP. If such a stream were to dry up in one year enough to stop all of the plants producing nectar and pollen for even just part of the summer, then it could kill all of the local bumblebees. If the area with the stream were sufficiently isolated from bumblebee re-colonization in subsequent years by extensive areas of high relief and unsuitable arid habitat (as appears to be the case at our sites in Zaskar, Ladakh and the Kunlun Pass), then interruption of stream flow could result in sudden, complete and permanent collapse of bumblebee populations throughout these valleys. Decrease in food availability is the most common mode by which climate change is believed to cause extinction (Cahill *et al.*, 2012). Thus bumblebees could be vulnerable to climate change affecting a different elevation zone from the one in which they live.

Climate change in mountain regions is also expected to cause elevational shifts in bumblebee ranges, with the possible loss of some species (Kudo, 2013; Ploquin, Herrera, & Obeso, 2013; Pyke, Inouye, & Thomson, 2012). Widespread climate warming across the QTP has resulted in changes in the timing of the beginning, end and ultimately in the length of the summer growing season (Shrestha, Gautam, & Bawa, 2012; Yu *et al.*, 2010). This could adversely affect the founding of bumblebee colonies and could constrain the period for colony growth, both of which could present a threat to bumblebees. The pattern of change in the QTP varies between a delay in spring 'green-up' in the southwest (and also at higher elevations, most likely because of declining spring precipitation) and a contrasting advance in spring 'green-up' elsewhere, despite a region-wide temperature increase (Shen *et al.*, 2014). In European mountains, effects of climate warming on the flora are expected to be less in areas where precipitation increases concomitantly with temperature (Engler *et al.*, 2011). Our field surveys in Qinghai 2010–2013 show strong fluctuations in bumblebee

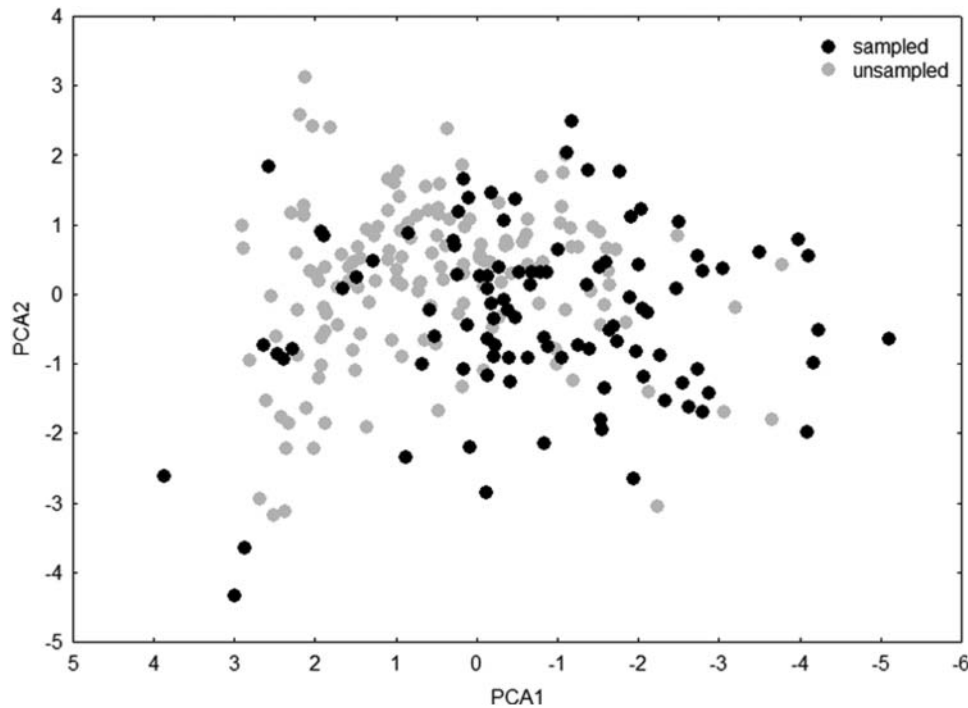


Fig. 14. PCA axes 1 and 2 (eigenvalues 2.87, 1.43) summarizing 71.7% of the variation in the six climate variables at the centroids for the QTP grid cells with centroids above 3000 m. Axis 1 is related to summer sunshine and rain (precipitation in the wettest month, irradiance in the warmest quarter, ratio of precipitation of the wettest month to precipitation of the warmest quarter, days of rain: Table 2); axis 2 is related to summer temperature and water deficit (mean temperature of the warmest quarter, water deficit: Table 2); similar to Fig. 12. The scale on the x-axis reversed, which preserves in the figure the approximate relative arrangement of the sites from geographic space (Figs 2, 12); sampled cells are shown as black spots; unsampled cells shown as grey spots.

numbers in some areas among years, but no systematic studies have been made so far.

Bumblebees in the wetter eastern QTP are believed to face threats from over-grazing. Frequent and intense summer grazing can reduce densities of the bumblebee-food-plant flowers and ultimately of the bumblebees themselves (Xie, Williams, & Tang, 2008). In some areas, a move away from traditional nomadic practices of summer yak grazing no longer allows breaks of several years for vegetation regeneration, so that in some areas (especially those with a fixed fence system) grazing now occurs every summer and intensively over large areas, posing a threat to the grasslands and to the bumblebees (Xie et al., 2008). In some areas of the QTP, bumblebee food plants find refuges from grazing animals on steep slopes, among boulder scree, or by carrying long sharp spines (e.g. bushes of *Caragana*: Polunin & Stainton, 1984: 461).

Future sampling

The high diversity of social alpine bumblebees in the QTP is all the more remarkable because more than half of the QTP alpine one-degree grid cells (the grey area in Fig. 2) remain unsampled in the data used here (Fig. 3: 60% unsampled). We examined the current pattern of sampling

for bumblebees in relation to variation in the six climate variables used in the CCA among all QTP grid cells with centroids above 3000 m using principal components analysis (PCA). Figure 14 shows that the grid cells sampled for bumblebees are reasonably well scattered across the climate space, so that existing sampling is not strongly biased in this respect, even though gaps remain. To find the optimum choice of a set of cells as priorities to sample next, we might wish to choose cells that improve the coverage of different combinations of climate conditions (a climatic gap analysis), which should then favour different (perhaps unsampled) bumblebee species, or novel combinations of species if bumblebee species respond differently to climate, as seems likely from their broader distributions. To achieve this selection, we could use the discrete *p*-median technique from the facilities location literature (Faith & Walker, 1996; Love, Morris, & Wesolowsky, 1988). This chooses cells to minimize the average distance from all remaining unsampled cells to their nearest sampled cells within the climate space. But simply by inspection of Fig. 14, unsampled cells in gaps in the west (left), north (top), and centre of the QTP are likely to be among the highest priorities for further sampling. This would improve our understanding of the overall pattern of compositional variation among QTP bumblebee faunas.

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Disclosure statement

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Supplemental data

Supplemental data for this article can be accessed here

References

- An, J.-D., Huang, J.-X., Shao, Y.-Q., Zhang, S.-W., Wang, B., Liu, X.-Y., ... Williams, P. H. (2014). The bumblebees of North China (Apidae, *Bombus* Latreille). *Zootaxa*, 3830, 1–89. doi: <http://dx.doi.org/10.11646/zootaxa.3830.1.1>
- An, J.-D., Williams, P. H., Miao, Z.-Y., & Zhou, B.-F. (2011). The bumblebees of Gansu, northwest China (Hymenoptera, Apidae). *Zootaxa*, 2865, 1–36.
- An, Z., Kutzbach, J. E., Prell, W. L., & Porter, S. C. (2001). Evolution of Asian monsoons and phased uplift of the Himalaya–Tibetan plateau since Late Miocene times. *Nature*, 411, 62–66.
- Anonymous. (2001). *The Times comprehensive atlas of the world* (10th ed.). London: Times Books.
- Biesmeijer, J. C., Roberts, S. P. M., Reemer, R., Ohlemüller, R., Edwards, M., Peeters, T., ... Kunin, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313, 351–354.
- Bingham, C. T. (1897). *The fauna of British India, including Ceylon and Burma. Hymenoptera*. (Vol. I). Wasps and bees. London: Taylor & Francis.
- Bischoff, H. (1936). Schwedisch-chinesische wissenschaftliche Expedition nach den nordwestlichen Provinzen Chinas, unter Leitung von Dr. Sven Hedin und Prof. Sü Ping-chang. Insekten gesammelt vom schwedischen Arzt der Expedition Dr. David Hummel 1927–1930. 56. Hymenoptera. 10. Bombinae. *Arkiv för zoologi*, 27A, 1–27.
- Bretschneider, E. (1981). *History of European botanical discoveries in China* (Vol. 2). Leipzig: Zentral-Antiquariat der DDR.
- Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Ryu, H. Y., ... Wiens, J. J. (2012). How does climate change cause extinction? *Proceedings of the Royal Society of London (B)*, doi: 10.1098/rspb.2012.1890, 1–10.
- Cameron, S. A., Hines, H. M., & Williams, P. H. (2007). A comprehensive phylogeny of the bumble bees (*Bombus*). *Biological Journal of the Linnean Society*, 91, 161–188.
- Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., & Griswold, T. L. (2011). Patterns of wide-spread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 662–667.
- Chang, D. H. S. (1981). The vegetation zonation of the Tibetan plateau. *Mountain Research and Development*, 1, 29–48.
- Cockerell, T. D. A. (1910). Some bees from high altitudes in the Himalaya mountains. *Entomologist*, 43, 238–239.
- Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S.-Y., Mao, C.-X., Chazdon, R. L., & Longino, J. T. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology*, 5, 3–21.
- Connor, E. F., & McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *American Naturalist*, 113, 791–833.
- Dupont-Nivet, G., Krijgsman, W., Langereis, C. G., Abels, H. A., Dai, S., & Fang, X.-M. (2007). Tibetan plateau aridification linked to global cooling at the Eocene-Oligocene transition. *Nature*, 445, 635–638.
- Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araújo, M. B., ... Guisan, A. (2011). 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, 17, 2330–2341.
- Faith, D. P., & Walker, P. A. (1996). Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiversity and Conservation*, 5, 399–415.
- Friese, H. (1905). Neue oder wenig bekannte Hummeln des russischen Reiches (Hymenoptera). *Ezhogodnik Zoologicheskago muzeya*, 9, 507–523.
- Friese, H. (1909). Neue Varietäten von *Bombus* (Hym.). *Deutsche entomologische Zeitschrift*, 1909, 673–676.
- Friese, H. (1918). Über Hummelformen aus dem Himalaja. *Deutsche entomologische Zeitschrift*, 1918, 81–86.
- Frison, T. H. (1935). Records, notes and descriptions of *Bremus* from Asia (Bremidae: Hymenoptera). *Record of the Indian Museum*, 37, 339–363.
- Fürst, M. A., McMahon, D. P., Osborne, J. L., Paxton, R. J., & Brown, M. J. F. (2014). Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature*, 506, 364–366.
- Gardner, A. S., Moholdt, G., Cogley, J. G., Wouters, B., Arendt, A. A., Wahr, J., ... Paul, F. (2013). A reconciled estimate of glacier contributions to sea level rise: 2003 to 2009. *Science*, 340, 852–857.
- Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379–391.
- Goulson, D. (2010). *Bumblebees, behaviour, ecology, and conservation* (2 ed.). Oxford: Oxford University Press.
- Heck, K. L., Belle, G. V., & Simberloff, D. (1975). Explicit calculation of the rarefaction diversity measurement and the

- determination of sufficient sample size. *Ecology*, 56, 1459–1461.
- Heinrich, B. (1979). *Bumblebee economics*. Cambridge (Massachusetts): Harvard University Press.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978.
- Hill, M. O. (2012). *DECORANA and TWINSpan, for ordination and classification of multivariate species data: a partially revised edition, together with supporting programs*, in Fortran 77. Wallingford: Centre for Ecology and Hydrology. Retrieved from: <http://www.ceh.ac.uk/products/software/cehsoftware-decoranatwinspace.htm>, accessed 27 October 2014.
- IPCC. (2014). *Climate change 2014: impacts, adaptation, and vulnerability*. Working Group II contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (<http://www.ipcc-wg2.gov/AR5/report/>, accessed 27 October 2014).
- Kääb, A., Berthier, E., Nuth, C., Gardelle, J., & Arnaud, Y. (2012). Contrasting patterns of early twenty-first-century glacier mass change in the Himalayas. *Nature*, 488, 495–498.
- Korup, O., & Montgomery, D. R. (2008). Tibetan plateau river incision inhibited by glacial stabilization of the Tsangpo gorge. *Nature*, 455, 786–789.
- Kriticos, D. J., Webber, B. L., Leriche, A., Ota, N., Macadam, I., Bathols, J., & Scott, J. K. (2012). CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution*, 3, 53–64.
- Kudo, G. (2014). Vulnerability of phenological synchrony between plants and pollinators in an alpine ecosystem. *Ecological Research* 29, 571–581. doi: 10.1007/s11284-013-1108-z (accessed online 2014).
- Legendre, P., & Legendre, L. (1998). *Numerical ecology* (2 ed.): Amsterdam and Oxford: Elsevier.
- Love, R. F., Morris, J. G., & Wesolowsky, G. O. (1988). *Facilities location. Models and methods*. London: North-Holland.
- Mao, L.-F., Chen, S.-B., Zhang, J.-L., Hou, Y.-H., Zhou, G.-S., & Zhang, X.-S. (2013). Vascular plant diversity on the roof of the world: spatial patterns and environmental determinants. *Journal of Systematics and Evolution*, 51, 371–381.
- Miao, Y.-F., Herrman, M., Wu, F.-L., Yan, X.-L., & Yang, S.-L. (2012). What controlled mid-late Miocene long-term aridification in Central Asia? – Global cooling or Tibetan plateau uplift: a review. *Earth-Science Reviews*, 112, 155–172.
- Morawitz, F. F. (1875). Bees. (Mellifera) *Reise in Turkestan, A. P. Fedtschenko. II Zoologischer Teil* (Vol. II, pp. ii+160). Moscow.
- Morawitz, F. F. (1883). Neue russisch-asiatische *Bombus*-Arten. *Trudy Russkago éntomologicheskago obshchestva*, 17, 235–245.
- Morawitz, F. F. (1887). Insecta in itinere cl. N. Przewalskii in Asia centrali novissime lecta. I. Apidae. *Trudy Russkago éntomologicheskago obshchestva*, 20(1886), 195–229.
- New, M. J., Hulme, M., & Jones, P. D. (1999). Representing 20th century space-time climate variability. I: Development of a 1961–1990 mean monthly terrestrial climatology. *Journal of Climate*, 12, 829–856.
- Panfilov, D. V. (1957). [On the geographical distribution of bumblebees (*Bombus*) in China]. *Acta geographica sinica*, 23, 221–239.
- Peres-Nato, P. R., & Jackson, D. A. (2001). How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia*, 129, 169–178.
- Ploquin, E. F., Herrera, J. M., & Obeso, J. R. (2013). Bumblebee community homogenization after uphill shifts in montane areas of northern Spain. *Oecologia*, 173, 1649–1660.
- Polunin, O., & Stainton, A. (1984). *Flowers of the Himalaya*. Oxford: Oxford University Press.
- Pyke, G. H., Inouye, D. W., & Thomson, J. D. (2012). Local geographic distributions of bumble bees near Crested Butte, Colorado: competition and community structure revisited. *Environmental Entomology*, 41, 1332–1349.
- Qiu, J. (2008). The third pole. *Nature*, 454, 393–396.
- Radoszkowski, O. (1860). Sur quelques hyménoptères nouveaux ou peu connus de la collection du Musée de l'Académie des sciences de St. Pétersbourg. *Byulleten' Moskovskogo obshchestva ispytatelei prirody*, 32(1859), 479–486.
- Rasmont, P. (1988). Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hyménoptera, Apidae, Bombinae). Ph. D., Gembloux.
- Reinig, W. F. (1930). Untersuchungen zur Kenntnis der Hummelfauna des Pamir-Hochlandes. Zoologische Ergebnisse der deutsch-russischen Alai-Pamir-Expedition der Notgemeinschaft der Deutschen Wissenschaft und der Akademie der Wissenschaften der U.d.S.S.R. *Zeitschrift für Morphologie und Ökologie der Tiere*, 17, 68–123.
- Reinig, W. F. (1940). Beiträge zur Kenntnis der Hummelfauna von Afghanistan. (Hym., Apid.). (Ergebnisse der Reise von H. und E. Kotsch in den Hindukusch im Jahre 1936.). *Deutsche entomologische Zeitschrift*, 1940, 224–235.
- Richards, O. W. (1928). On a collection of humble-bees (Hymenoptera, Bombidae) made in Ladakh by Col. R. Meinertzhagen. *Annals and Magazine of Natural History* (10), 2, 333–336.
- Richards, O. W. (1930). The humble-bees captured on the expeditions to Mt. Everest (Hymenoptera, Bombidae). *Annals and Magazine of Natural History* (10), 5, 633–658.
- Shen, M.-G., Zhang, G.-X., Cong, N., Wang, S.-P., Kong, W.-D., & Piao, S.-L. (2014). Increasing altitudinal gradient of spring vegetation phenology during the last decade on the Qinghai-Tibetan Plateau. *Agricultural and Forest Meteorology*, 189–190, 71–80.
- Shrestha, U. B., Gautam, S., & Bawa, K. S. (2012). Widespread climate change in the Himalayas and associated changes in local ecosystems. *Public Library of Science ONE*, 7, 1–10.
- Skorikov, A. S. (1910). [Intraspecific forms of *Bombus mendax* Gerst.] (Hymenoptera, Bombidae). *Russkoe éntomologicheskoe Obozrénie*, 9(1909), 328–330.
- Skorikov, A. S. (1912). Neue Hummelformen (Hymenoptera, Bombidae). IV. *Russkoe éntomologicheskoe Obozrénie*, 12, 606–610.
- Skorikov, A. S. (1914a). Les formes nouvelles des bourdons (Hymenoptera, Bombidae). VI. [1914a]. *Russkoe éntomologicheskoe Obozrénie*, 14, 119–129.
- Skorikov, A. S. (1914b). *Pratobombus leucopygos* [sic] (F. Mor.) et ses variations (Hymenoptera, Bombidae). [1914b]. *Russkoe éntomologicheskoe Obozrénie*, 14, 293–294.
- Skorikov, A. S. (1931). Die Hummelfauna Turkestans und ihre Beziehungen zur zentralasiatischen Fauna (Hymenoptera, Bombidae). In V. A. Lindholm (Ed.), *Abhandlungen der Pamir-Expedition 1928* (Vol. 8, pp. 175–247). Leningrad: Academy of Sciences of the USSR.
- Skorikov, A. S. (1933a). Zur Fauna und Zoogeographie der Hummeln des Himalaya. [1933b]. *Doklady Akademii nauk SSSR*, 1933, 243–248.
- Skorikov, A. S. (1933b). Zur Hummelfauna Japans und seiner Nachbarländer. [1933a]. *Mushi*, 6, 53–65.

- Smith, F. (1852). Descriptions of some hymenopterous insects from northern India. *Transactions of the Entomological Society of London*, 2, 45–48.
- Smith, F. (1871). Descriptions of some new insects collected by Dr. Anderson during the expedition to Yunan [sic]. *Proceedings of the Zoological Society of London*, 1871, 244–249.
- Smith, F. (1879). *Descriptions of new species of Hymenoptera in the collection of the British Museum*. London: Trustees of the British Museum.
- Tkalců, B. (1961). Zur Hummelfauna der Umgebung Kuku-Nors (Hymenoptera, Bombinae). *Casopis Československé společnosti entomologické*, 58, 344–379.
- Tkalců, B. (1968). Neue Arten der Unterfamilie Bombinae der paläarktischen Region (Hymenoptera, Apoidea). *Sborník Entomologického oddelení Národního musea v Praze*, 65, 21–51.
- Tkalců, B. (1969). Beiträge zur Kenntnis der Fauna Afghanistans (Sammelergebnisse von O. Jakes 1963–64, D. Povolny 1965, D. Povolny & Fr. Tenora 1966, J. Simek 1965–66, D. Povolny, J. Geisler, Z. Sebek & Fr. Tenora 1967). *Bombinae, Apoidea, Hym.* *Casopis Moravského musea v Brne*, 53, 189–210.
- Tkalců, B. (1974). Ergebnisse der 1. und 2. mongolisch-tschechoslowakischen entomologisch-botanischen Expedition in der Mongolei. Nr. 29: Hymenoptera, Apoidea, Bombinae. *Sborník faunistických prací Entomologického oddelení Národního musea v Praze*, 15, 25–57.
- Velthuis, H. H. W., & Doorn, A. v. (2006). A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. *Apidologie*, 37, 421–451.
- Vogt, O. (1908). *Bombi (Hummeln). Wissenschaftliche Ergebnisse von Expedition Filchner nach China und Tibet 1903–1905, X. Band – I. Teil, 1. Abschnitt: Zoologische Sammlungen* (pp. 100–101). Berlin: Mittler & Sohn.
- Vogt, O. (1911). Studien über das Artproblem. 2. Mitteilung. Über das Variieren der Hummeln. 2. Teil. (Schluss). *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin*, 1911, 31–74.
- Wang, C.-Z., Guo, H.-D., Zhang, L., Qiu, Y.-B., Sun, Z.-C., Liao, J.-J., ... Zhang, Y.-L. (2013). Improved alpine grassland mapping in the Tibetan Plateau with MODIS time series: a phenology perspective. *International Journal of DigitalEarth*. doi: 10.1080/17538947.2013.860198
- Wang, S.-F. (1979). Three new species of bumble [sic] bees from Tibet. *Acta entomologica sinica*, 22, 188–191.
- Wang, S.-F. (1982). Hymenoptera: Apidae – *Bombus*. In *Insects of Xizang* (Vol. II, pp. 427–447). Beijing: Science Press.
- Wang, S.-F. (1988). Hymenoptera: apidae – genus *Bombus*. In F. Huang (Ed.), *Insects of Mt. Namjagbarwa region of Xizang* (pp. 553–557). Beijing: Science Press.
- Wang, S.-F., & Yao, J. (1996). Hymenoptera: apidae [sic] – Bombini. In: Huang F.-S., ed. *Insects of the Karakorum-Kunlun mountains* (pp. 303–309). Beijing: Science Press.
- Whitehorn, P. R., O'Connor, S., Wackers, F. L., & Goulson, D. (2012). Neonicotinoid pesticide reduces bumble bee colony growth and queen production. *Science*, 336, 351–352.
- Williams, P. H. (1991). The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini). *Bulletin of the British Museum (Natural History) (Entomology)*, 60, 1–204.
- Williams, P. H. (1996). Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings of the Royal Society of London (B)*, 263, 579–588.
- Williams, P. H. (1998). An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). *Bulletin of The Natural History Museum (Entomology)*, 67, 79–152 [updated at <http://www.nhm.ac.uk/bombus/> accessed 27 October 2014].
- Williams, P. H. (2000). Some properties of rarity scores used in site quality assessment. *British Journal of Entomology and Natural History*, 13, 73–86.
- Williams, P. H. (2007). The distribution of bumblebee colour patterns world-wide: possible significance for thermoregulation, crypsis, and warning mimicry. *Biological Journal of the Linnean Society*, 92, 97–118.
- Williams, P. H. (2011). Bumblebees collected by the Kyushu University Expeditions to Central Asia (Hymenoptera, Apidae, genus *Bombus*). *Esakia*, 50, 27–36.
- Williams, P. H., An, J.-D., & Huang, J.-X. (2011). The bumblebees of the subgenus *Subterraneobombus*: integrating evidence from morphology and DNA barcodes (Hymenoptera, Apidae, *Bombus*). *Zoological Journal of the Linnean Society*, 163, 813–862.
- Williams, P. H., An, J.-D., Huang, J.-X., & Yao, J. (2010). BBCE: A new initiative to document Chinese bumble bees for pollination research. *Journal of Apicultural Research*, 49, 221–222.
- Williams, P. H., Brown, M. J. F., Carolan, J. C., An, J.-D., Goulson, D., Aytekin, A. M., ... Xie, Z.-H. (2012). Unveiling cryptic species of the bumblebee subgenus *Bombus s. str.* world-wide with COI barcodes (Hymenoptera: Apidae). *Systematics and Biodiversity*, 10, 21–56. doi: 10.1080/14772000.2012.664574
- Williams, P. H., & Cameron, S. A. (1993). Bumble bee (*Bombus* Latr.) records from the Valley of Flowers, Uttar Pradesh. *Bulletin of Entomology*, 31, 125–127.
- Williams, P. H., Cameron, S. A., Hines, H. M., Cederberg, B., & Rasmont, P. (2008). A simplified subgeneric classification of the bumblebees (genus *Bombus*). *Apidologie*, 39, 46–74.
- Williams, P. H., de Klerk, H. M., & Crowe, T. M. (1999). Interpreting biogeographical boundaries among Afrotropical birds: spatial patterns in richness gradients and species replacement. *Journal of Biogeography*, 26, 459–474.
- Williams, P. H., & Gaston, K. J. (1998). Biodiversity indicators: graphical techniques, smoothing and searching for what makes relationships work. *Ecography*, 21, 559–568.
- Williams, P. H., Ito, M., Matsumura, T., & Kudo, I. (2010). The bumblebees of the Nepal Himalaya (Hymenoptera: Apidae). *Insecta Matsumurana*, 66, 115–151.
- Williams, P. H., & Osborne, J. L. (2009). Bumblebee vulnerability and conservation world-wide. *Apidologie*, 40, 367–387.
- Williams, P. H., Tang, Y., Yao, J., & Cameron, S. (2009). The bumblebees of Sichuan (Hymenoptera: Apidae, Bombini). *Systematics and Biodiversity*, 7, 101–190. doi: 10.1017/S1477200008002843
- Williams, P. H., Thorp, R. W., Richardson, L. L., & Colla, S. R. (2014). *Bumble bees of North America. An identification guide*. Princeton New Jersey: Princeton University Press.
- Xie, Z.-H., Williams, P. H., & Tang, Y. (2008). The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. *Journal of Insect Conservation*, 12, 695–703. doi: 10.1007/s10841-008-9180-3
- Xu, J.-C., Grumbine, R. E., Shrestha, A., Erikson, M., Yang, X.-F., Wang, Y., & Wilkes, A. (2009). The melting Himalayas:

- cascading effects of climate change on water, biodiversity, and livelihoods. *Conservation Biology*, 23, 520–530.
- Yu, H.-Y., Luedeling, E., & Xu, J.-C. (2010). Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings National Academy of Science*, 107, 22151–22156.
- Zhang, L., Guo, H.-D., Ji, L., Wang, C.-Z., Yan, D.-M., Li, B., & Li, J. (2013). Vegetation greenness trend (2000 to 2009) and the climate controls in the Qinghai-Tibetan Plateau. *Journal of Applied Remote Sensing*, 7. doi: 10.1117/1.JRS.7.073572.

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