



Evidence of Bumble Bee Extirpation and Colonization, Galiano Island, British Columbia, Canada

Authors: Simon, Andrew D. F., Best, Lincoln R., and Starzomski, Brian M.

Source: Northwest Science, 96(3-4) : 206-219

Published By: Northwest Scientific Association

URL: <https://doi.org/10.3955/046.096.0305>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Andrew D. F. Simon¹, School of Environmental Studies, University of Victoria, PO Box 1700 STN CSC, Victoria, British Columbia V8W 2Y2 Canada

Lincoln R. Best, Department of Horticulture, Oregon State University, 2750 SW Campus Way, Corvallis, OR 97331

Brian M. Starzomski, School of Environmental Studies, University of Victoria, PO Box 1700 STN CSC, Victoria, British Columbia V8W 2Y2 Canada

Evidence of Bumble Bee Extirpation and Colonization, Galiano Island, British Columbia, Canada

Abstract

We present evidence for historical change in a bumble bee community on Galiano Island, British Columbia, Canada, including the probable extirpation of three bumble bee species—*Bombus insularis* Smith, *B. occidentalis* Greene, and *B. suckleyi* Greene—as well as the disappearance of two species represented by singletons in the historical record: *B. fervidus* Fabricius and *B. flavidus* Eversmann. Evidence is based on a comparison of historical and contemporary species occurrence data, including recent data from intensive sampling targeting bumble bees using blue vane traps. The decline of *B. occidentalis* in southern portions of its range has long been observed, yet to our knowledge this is the first established case of its probable extirpation within an extensively surveyed part of its range. Results indicate that an additional species, *B. vosnesenskii* Radoszkowski, is a recent arrival on Galiano Island and has been expanding its range concurrently with the decline of *B. occidentalis*. Elsewhere in the region *B. vosnesenskii* has become a dominant species, particularly in urban environments. However, our data show it to be the least abundant species on this largely forested island. We also report patterns in the occurrence of *B. sitkensis* Nylander and *B. vosnesenskii*, suggesting that niche segregation may confound the effect of competitive exclusion previously reported for these species. Potential factors contributing to this likely case of bumble bee extirpation and subsequent colonization are discussed in the context of Galiano Island's historical land use and ecology. In conclusion, we assess the potential for community science to aid in the detection of ecological change via comparison of historical baseline and contemporary crowd-sourced biodiversity data.

Keywords: bumble bee community ecology, extirpation, colonization, rarefaction, ecological change

Introduction

Worldwide, bumble bees face increasing threats associated with climate and anthropogenic landscape change, which have resulted in numerous population declines and species range restrictions (Szabo et al. 2012, Sanchez-Bayo and Goka 2014, Kerr et al. 2015, Biella et al. 2017, Guzman et al. 2021). In western North America, *Bombus occidentalis* Greene is a well-established case of species' decline, with declines reported throughout some southern portions of its range over the last several decades (Colla and Ratti 2010, Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2014). The decline of *B. occidentalis*

has largely been attributed to pathogens associated with commercial rearing of bumble bees in industrial agricultural settings, including the parasitic fungus *Vairimorpha bombi* (Fantham & Porter) Tokarev et al. (Rao and Stephen 2007, Otterstatter and Thomson 2008, Colla and Ratti 2010, COSEWIC 2014, Graystock et al. 2016, Grupe and Quandt 2020). Cuckoo bumble bees (subgenus *Psithyrus*) associated with *B. occidentalis* and other bumble bee species are also in decline, signaling their vulnerability to fluctuations in host population densities (Antonovics and Edwards 2011, Williams et al. 2014, Hatfield et al. 2015a).

Alongside the decline of *B. occidentalis*, another bumble bee species—*B. vosnesenskii* Radoszkowski—has undergone significant range expansion in coastal western British Columbia (Fraser et al. 2012). Research suggests this

¹Author to whom correspondence should be addressed.
Email: adfsimon@imerss.org

species has come to occupy the niche left vacant by *B. occidentalis*, showing high potential for colonization, particularly in urban environments where its dominance has been associated with declines among other bumble bee species such as *B. sitkensis* Nylander (McFrederick and LeBuhn 2006, Fraser et al. 2012, Cole et al. 2019).

Here we present evidence for historical change in an insular bumble bee community, establishing the probable extirpation of *B. insularis* (Smith), *B. occidentalis*, and *B. suckleyi* Greene from Galiano Island, British Columbia, Canada, and the island's recent colonization by *B. vosnesenskii*. We also assess the disappearance of two additional species—*B. fervidus* (Fabricius) and *B. flavidus* Eversmann—represented by singletons in the historical record. Evidence for these changes is based on the rarefaction of: 1) historical species occurrence data; 2) data collected through intensive sampling using blue vane traps; and 3) observations on the community-science platform iNaturalist (2022). Set against the backdrop of Galiano Island's land-use history, these results corroborate previous findings concerning the causes of bumble bee species declines and provide further insight into the ecology of *B. sitkensis* and *B. vosnesenskii*.

Methods

Study Area

Galiano Island lies in the rain shadow of the Olympic Mountains and the Vancouver Island Ranges, in southern coastal British Columbia, Canada, a region defined by its temperate Mediterranean-type climate, with mild, wet winters and warm, dry summers (Klassen et al. 2015). The combined effects of low precipitation, warm temperatures, and high sunshine hours result in an annual moisture deficit during summer months, which varies depending on precipitation (Moore et al. 2010). Galiano Island remains relatively intact ecologically, with about 24% of its land base conserved in protected areas (Island Trust Conservancy [ITC] 2018). Today, 78% of the island landscape remains forested, with only 9% converted for active human use, including rural development and limited small-scale agriculture (Emmings and Erickson 2004; Madrone Envi-

ronmental Services Ltd [MES] 2008, 2017; ITC 2018), though forestry and cumulative land-use effects have altered habitats here, as throughout the rest of British Columbia (Shackelford et al. 2018). Approximately 60% of the forested land base comprises regenerating early seral and young forests with dense canopy structure; the remainder is in a mature to old-growth state (Emmings and Erickson 2004). Galiano Island's forests are mostly coniferous, composed primarily of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western redcedar (*Thuja plicata* Donn ex D. Don), and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), with pockets of moist deciduous forests and dry woodlands, including bigleaf maple (*Acer macrophyllum* Pursh), red alder (*Alnus rubra* Bong.), arbutus (*Arbutus menziesii* Pursh), and Garry oak (*Quercus garryana* Douglas ex Hook.), species representative of British Columbia's Coastal Douglas-fir Biogeoclimatic Zone (Klassen et al. 2015).

Bumble Bee Sampling and Analysis

We sampled bumble bees as part of an ecological study investigating the impact of seasonal drought on plant-pollinator communities (Simon et al. 2021). Bumble bees were collected using blue vane traps (Stephen and Rao 2005) systematically distributed across the landscape in a 2 × 2 factorial study design contrasting dry versus wet, and disturbed versus undisturbed, site conditions. However, there was an imbalance in the study design due to difficulties in logistics of site selection and access. We selected field sites and stratified site conditions using terrestrial ecosystem mapping data (MES 2008), spanning a broad range of habitats representative of the Coastal Douglas-fir Biogeoclimatic Zone (Nuszdorfer et al. 1991), including woodlands and associated rock outcrop communities, wetlands, clearcuts, hydro-line corridors, gardens, orchards, and fields. Sites ranged in size from 0.21 to 6.3 ha and were spaced between approximately 0.5 km and 23 km apart (Figure 1). Sampling was conducted over five sample periods, from April through August 2018, across 24 field sites, with three blue vane traps allocated to each site (representing a single sample), resulting in 119 samples (120 less one

sample compromised due to human interference) representing 47,896 individuals. Each sampling period lasted 11 days—the time required to concurrently estimate floral resources at each site. We modelled the abundance of each bumble bee species as a response to habitat types and other environmental variables using generalized linear mixed models (GLMMs) implemented using ‘lme4’, and ‘glmmTMB’ in cases where zero-inflation proved problematic (Bates et al. 2015, Brooks et al. 2017). Note, however, that estimates of floral resources and other aspects of the ecological study conducted in 2018 are not relevant to our analysis of historical change and are therefore not reported as results.

Analysis of Historical Change

Two sources of contemporary species occurrence data were compared with historical occurrence data to inform our analysis of historical change in these communities. These include: 1) specimens ($n = 47,896$) collected from Galiano Island using blue vane traps during our 2018 ecological study, as described above; and 2) iNaturalist (2022) observations of the local bumble bee fauna ($n = 238$), dating from 2016 to 2021. All material, including historical voucher specimens, were carefully reviewed, and species determined with reference to Williams et al. (2014).

Historical species occurrence data are based on voucher specimens ($n = 278$) dated from 1970 to 2010, deposited at the Beaty Biodiversity Museum in Vancouver, BC, Canada, and at the Royal British Columbia Museum (RBCM) in Victoria, BC. A total of 285 specimens were databased in collections. However, 6 specimens at the RBCM were only determined to genus and could not be located during our visit to the collection. One specimen was dated to 2017 and thus was not included among historical records. No other Galiano Island bumble bee collections exist as far as the authors are aware. Historical metadata indicate that specimens analysed in this study were collected by flight intercept traps ($n = 193$), aerial netting ($n = 10$), light traps ($n = 3$), pitfall traps ($n = 3$), window traps ($n = 2$), and otherwise unknown methods ($n = 67$). The

distribution of historical and contemporary species occurrence data are presented in Figure 1. Data from 2018 blue vane samples, including catalog numbers for synoptic collections deposited at the RBCM, are summarized in Table 1. Data and R scripts for implementing analyses are available on Dryad (2023). Historical and contemporary species occurrence data were analysed by rarefaction using ‘vegan’, R package v.2.5–5 (Oksanen et al. 2019, R Core Team 2019) and the Chao2 estimator (Chao 1984) implemented using ‘fossil’ (Vavrek 2011) to estimate species richness, that is, the number of unique species occurring within historical and contemporary communities. We then compared the similarity of rarefaction curves using the R package ‘rareNMtests’ v.1.1 (Cayuela and Gotelli 2014), testing the differences in historical and contemporary species assemblages based on null models. To do this, we followed the ecological null hypothesis test procedure outlined in Cayuela et al. (2015), which reveals whether samples are more different than would be expected if they were drawn from a single underlying assemblage. The same null model test was applied to compare rarefaction curves based on iNaturalist observations with those generated from blue vane trap samples, to determine whether these two sampling methods reliably converged on estimates of species richness for the contemporary bumble bee community. In these tests, Z scores represent the cumulative area between the observed sample rarefaction curve and the composite rarefaction curve; P -values represent the probability of Z given the distribution of simulated Z values; low P -values imply that observed differences among samples in species composition, richness and/or relative abundance are improbable if the samples were drawn from the same assemblage (Cayuela and Gotelli 2014). For historical data, we used individual-based rarefaction to implement null model tests comparing rarefaction of historical data with rarefaction of data from iNaturalist observations and blue vane samples. While historical voucher specimens may be analysed as sample-based data, we followed Osazuwa-Peters et al. (2018) in treating these data as individual-based to control for differences in random sampling effort and to facilitate comparison of rarefaction curves using null model tests.

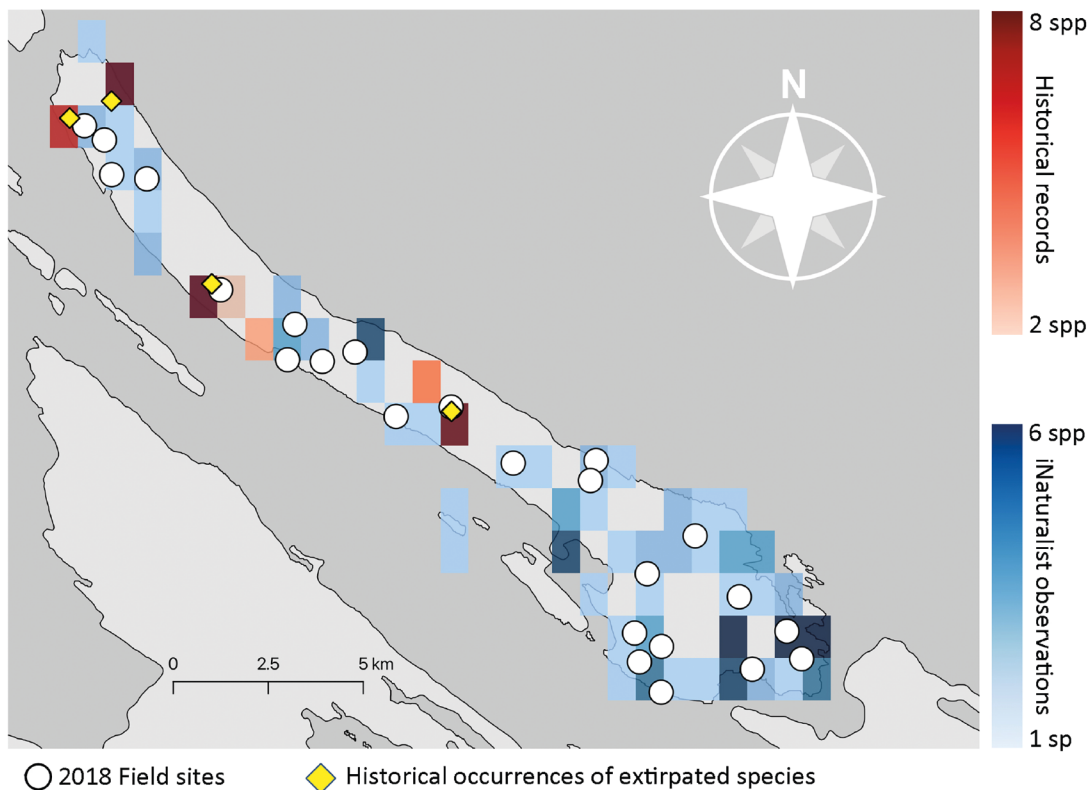


Figure 1. Choropleth map of bumble bee species richness based on historical records (1970 to 2010) and recent iNaturalist observations (2016 to 2021) from Galiano Island, BC, Canada. Field sites from 2018 surveys are also indicated, as well as historical collection sites for three bumble bee species (*Bombus insularis*, *B. occidentalis*, and *B. suckleyi*) reported as extirpated in this study, and two species represented by singletons in the historical record (*B. fervidus*, *B. flavidus*). The six species (*B. flavifrons*, *B. melanopygus*, *B. mixtus*, *B. sitkensis*, *B. vancouverensis*, *B. vosnesenskii*) presently known to Galiano Island were widespread in 2018, occurring in samples from all 24 field sites. Grid scale = 0.01°; at this latitude, each cell represents about 82 ha.

Taking this approach, bumble bees collected by blue vane traps were necessarily treated as individuals ($n = 47,896$) for comparison with individual-based rarefaction curves in null model tests, though a sample-based curve was also considered for these data, which converged on the same estimate of species richness.

Results

Ten bumble bee species were historically reported for Galiano Island, represented by 278 specimens in research collections: 1) *Bombus fervidus*; 2) *B. flavidus*; 3) *B. flavifrons* Cresson; 4) *B. insularis*; 5) *B. melanopygus* Nylander; 6) *B. mixtus* Cresson; 7) *B. occidentalis*; 8) *B. sitkensis*; 9) *B. suckleyi*;

and 10) *B. vancouverensis* Cresson. Of these ten species collected from 1970 to 2010, only five have since been detected. The other five species—*B. fervidus*, *B. flavidus*, *B. insularis*, *B. occidentalis*, and *B. suckleyi*—have not been detected through recent sampling (from 2016 to 2021). *Bombus fervidus* is represented by a single individual in historical collections, collected in 1985; *B. flavidus* is also represented by a single individual collected in 1981. These two singletons belong to a series of collections made on Galiano Island by G. G. E. Scudder and S. G. Cannings and have been verified as reliable records (Sydney G. Cannings, Environment Canada, personal communication; see supplemental material, available online only).

TABLE 1. Counts of bumble bee individuals sampled in 2018 blue vane surveys, summarized by species, caste (♀ = queen; ♀ = worker; ♂ = male), and monthly sampling periods. Catalog numbers are listed for specimens deposited at the Royal British Columbia Museum. Note catalog numbers refer to a synoptic sample of each species, including representatives of all castes.

	Caste	APR	MAY	JUN	JUL	AUG	Total	Catalog # (ENT021)
<i>B. flavifrons</i>	♀	405	1,772	369	161	94	2,801	012788, 012789, 012790,
	♀	0	160	273	1,432	115	1,980	012791, 012792, 012793,
	♂	0	4	36	696	105	841	012794, 012795, 012796
<i>B. melanopygus</i>	♀	147	128	169	70	31	545	012780, 012781, 012782,
	♀	1	1,078	3,126	98	3	4,306	012783, 012784, 012785,
	♂	0	38	378	47	2	465	012786, 012787
<i>B. mixtus</i>	♀	757	926	183	305	98	2,269	012798, 012799, 012800,
	♀	0	934	1,959	1,347	22	4,262	012801, 012802, 012803,
	♂	0	3	69	382	5	459	012804, 012805, 012806
<i>B. sitkensis</i>	♀	1,002	543	193	387	106	2,231	012807, 012808, 012809,
	♀	2	1,216	1,968	1,036	17	4,239	012810, 012811, 012812,
	♂	0	101	396	380	9	886	012813, 012814, 012815
<i>B. vancouverensis</i>	♀	1,035	1,770	386	158	160	3,509	012771, 012772, 012773,
	♀	0	1,645	6,023	9,490	271	17,429	012774, 012775, 012776,
	♂	0	2	183	702	40	927	012777, 012778, 012779
<i>B. vosnesenskii</i>	♀	60	234	39	2	10	345	012763, 012764, 012765,
	♀	0	64	151	142	28	385	012766, 012767, 012768,
	♂	0	0	13	3	1	17	012769, 012770

Bombus insularis ($n = 18$), *B. occidentalis* ($n = 9$), and *B. suckleyi* ($n = 26$) have not been observed on Galiano Island since 1990. An additional species, *B. vosnesenskii*, was reported locally for the first time in 2017 based on an iNaturalist observation (iNaturalist 2017) and subsequently confirmed through blue vane sampling. In this observation, the lateral view of the bumble bee permits the determination of *B. vosnesenskii* based on the absence of extensive yellow hairs on sternite 4, the short even hair of the dorsum, and the absence of dark hairs antero-medially on tergite 4, which rules out *B. caliginosus* Frison. The presence of *B. vosnesenskii* and absence of *B. caliginosus* on Galiano Island is supported by the determination of specimens collected through intensive blue vane sampling in 2018.

Six bumble bee species are currently known to occur on Galiano Island (Figure 2, Table 2). In 2018, we found that these six species occurred throughout all habitats, with little variability in community composition across the landscape (Table 3). Only two species varied significantly in

abundance between certain habitats: *B. sitkensis* was significantly more abundant in wet semi-natural habitats than in dry modified habitats ($IRR_{\text{WET.N.}} = 1.74_{\text{DRY.M.}}$, $P = 0.022$); conversely, *B. vosnesenskii* was significantly more abundant in dry modified habitats than in wet semi-natural habitats ($IRR_{\text{DRY.M.}} = 3.51_{\text{WET.N.}}$, $P < 0.001$). Wet modified habitats also hosted significantly more *B. vosnesenskii* individuals than in wet semi-natural habitats ($IRR_{\text{WET.M.}} = 2.49_{\text{WET.N.}}$, $P = 0.015$).

Rarefaction curves based on blue vane samples and iNaturalist bumble bee community data both reached an asymptote, predicting 6 species in the present-day community (Figure 2b, 2c). When treated as sample-based data, the rarefaction curve based on blue vane samples also reached an asymptote, converging on an estimate of 6 species in the contemporary community, though it was necessary to treat these data as individual-based for comparison with historical and iNaturalist data using null model tests. The rarefaction curve based on historical specimen data did not reach an asymptote at 278 iterations, as it was strongly

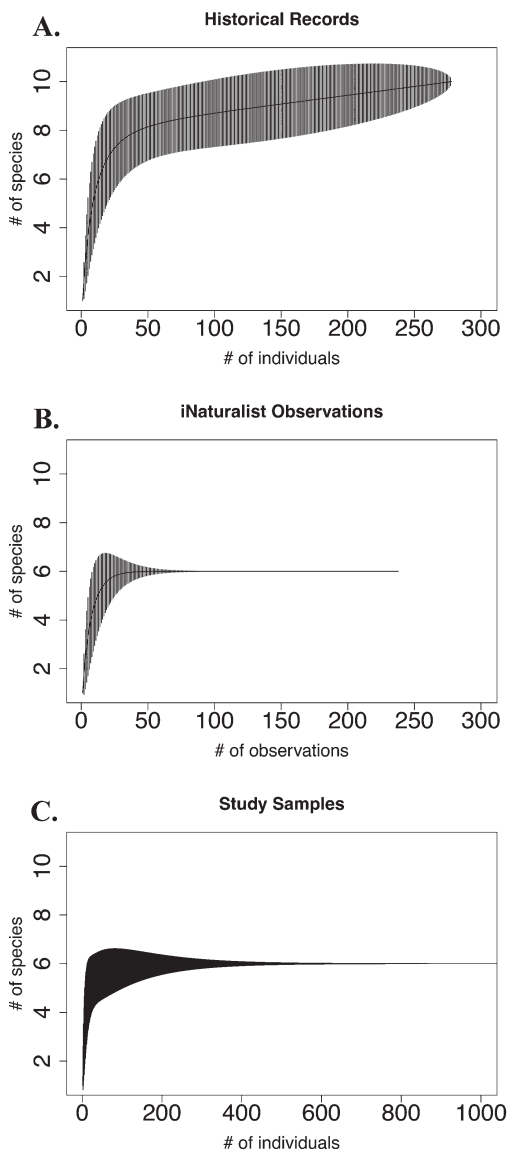


Figure 2. Individual-based rarefaction curves of bumble bee data, with 95% confidence intervals: A) Historical records (1970 to 2010, $n = 278$); B) iNaturalist observations (2016 to 2021, $n = 238$); C) Blue vane trap samples (2018, $n = 47,896$).

influenced by the two singleton occurrences of *B. fervidus* and *B. flavidus*, with the Chao2 estimator predicting 11 species in the historical bumble bee community (Figure 2a). When singletons were removed from the historical dataset, however, the

rarefaction curve reached an asymptote, estimating a richness of 8 species. Null models testing rarefaction curves based on blue-vane sampling ($Z = 182966.6$) and iNaturalist data ($Z = 796.8$) against the curve generated from historical data showed that the past community assemblage significantly differed from the present-day community ($P = 0.005$). The null model test comparing the rarefaction curve of iNaturalist observational data against the curve based on data from blue vane sampling ($Z = 52.4$) indicated that the community did not significantly differ ($P = 0.115$), confirming that samples were randomly drawn from the same underlying assemblage. This test, combined with rarefaction curves shown in Figure 2, indicate that survey efforts based on intensive *Bombus*-targeted sampling with blue vane traps, as well as efforts based on iNaturalist observations, were sufficient to estimate the richness of the contemporary bumble bee community.

Discussion

Extirpation: The Case of Galiano Island's Missing Bumble Bees

We documented significant shifts in the composition of an insular bumble bee community, with the apparent loss of half of the historically occurring fauna and the recent arrival of *Bombus vosnesenskii*, making Galiano Island an important case study in ecological change. These findings coincide with regional trends documenting the historical decline of *B. occidentalis* (Colla and Ratti 2010, COSEWIC 2014) and the subsequent expansion of *B. vosnesenskii* in British Columbia (Fraser et al. 2012).

The case for the extirpation of *B. fervidus*, *B. flavidus*, *B. insularis*, *B. occidentalis*, and *B. suckleyi* remains tentative, however, with several caveats to be considered. According to the International Union for Conservation of Nature (IUCN 2012), “a taxon is presumed Extinct (in our case, equivalent to Extirpated – locally extinct) when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should

TABLE 2. Specimen counts and proportional abundances of bumble bee species represented by: 1) historical collections; 2) iNaturalist observations; and 3) individuals captured in blue vane traps. Note: the proportional representation of *B. vosnesenskii* in iNaturalist observations contrasts strongly with what was found in blue vane samples, indicating a bias in community science observations toward disturbed environments (see Table 3).

Taxon	Historical specimens (1970–2010)		iNat observations (2016–2021)		Blue vane sampling (2018)	
	<i>n</i> = 278	Proportion	<i>n</i> = 238	Proportion	<i>n</i> = 47,896	Proportion
<i>Bombus fervidus</i>	1	< 0.01	—	—	—	—
<i>Bombus flavidus</i>	1	< 0.01	—	—	—	—
<i>Bombus flavifrons</i>	80	0.29	38	0.16	5,622	0.12
<i>Bombus insularis</i>	18	0.06	—	—	—	—
<i>Bombus melanopygus</i>	38	0.14	30	0.12	5,316	0.11
<i>Bombus mixtus</i>	53	0.19	23	0.10	6,990	0.15
<i>Bombus occidentalis</i>	9	0.03	—	—	—	—
<i>Bombus sitkensis</i>	18	0.06	24	0.10	7,356	0.15
<i>Bombus suckleyi</i>	26	0.09	—	—	—	—
<i>Bombus vancouverensis</i>	34	0.12	92	0.39	21,865	0.46
<i>Bombus vosnesenskii</i>	—	—	31	0.13	747	0.01

TABLE 3. Bumble bee community composition, expressed as the relative abundance of species per habitat type, based on intensive blue vane sampling from April through August 2018. Bumble bee species: *B. flav.* = *B. flavifrons*, *B. mel.* = *Bombus melanopygus*, *B. mix.* = *Bombus mixtus*, *B. sit.* = *Bombus sitkensis*, *B. van.* = *Bombus vancouverensis*, *B. vos.* = *Bombus vosnesenskii*.

Habitat type	Number of sites	Number of samples	Bumble bee species					
			<i>B. flav.</i>	<i>B. mel.</i>	<i>B. mix.</i>	<i>B. sit.</i>	<i>B. van.</i>	<i>B. vos.</i>
Dry semi-natural (woodlands, rock outcrops, meadows; DRY.N)	8	39	0.13	0.12	0.13	0.15	0.45	0.02
Dry modified (clearcuts, hydro-line corridors, etc.; DRY.M)	6	30	0.08	0.12	0.14	0.09	0.54	0.03
Wet semi-natural (wetlands; WET.N)	4	20	0.12	0.08	0.17	0.26	0.36	< 0.01
Wet modified (orchards, gardens, fields, etc.; WET.M)	6	30	0.13	0.11	0.17	0.17	0.42	0.01

be over a time frame appropriate to the taxon’s life cycle and life form.” The evidence we present, including one year of intensive blue vane sampling targeting *Bombus*, as well as multiple years of iNaturalist data, establishes the strong likelihood that at least five bumble bee species historically known to Galiano Island no longer occur. Our sampling focused on a diverse range of habitats representative of the island landscape (e.g., woodlands, wetlands, clearcuts, rural areas, and gardens, all within a forested matrix), including areas in the vicinity of historical collection

sites (Figure 1). Studies have consistently demonstrated blue vane traps to be highly effective at sampling large insects, particularly bumble bees, though additional sampling methods may be required to capture a complete picture of bee communities (Stephen and Rao 2005, 2007; Rao and Stephen 2007; Wilson et al. 2008; Geroff et al. 2014; Buchanan et al. 2017; Gibbs et al. 2017; McCravy and Ruhoff 2017; Rhoades et al. 2017). Studies have also shown blue vane traps to be effective at passively sampling the species concerned in this study, including *B. fervidus*,

B. flavidus, *B. insularis*, *B. occidentalis*, and *B. suckleyi* (Kimoto et al. 2012, Pampell et al. 2015, Rhoades et al. 2016, Gibbs et al. 2017, Rivers et al. 2018). Nevertheless, additional targeted sampling efforts may be necessary to conclusively establish this case of bumble bee extirpation.

Because historical collection efforts are spatially limited in extent, individual-based rarefaction of historical biological specimen data could be spatially biased. However, recent work has shown individual-based rarefaction to be preferable to spatially explicit rarefaction to control for differences in random sampling effort (Osazuwa-Peters et al. 2018). Moreover, recent sampling across a broad range of habitats revealed that bumble bee species comprising the contemporary fauna are relatively widespread on Galiano Island. Species occurred throughout all habitats, and community composition overall was relatively even across the landscape, though two species varied significantly in abundance between certain habitats. Bumble bees are known to have broad foraging ranges, from 1.5 km (Osborne et al. 2008) to as far as 11.6 km (Rao and Strange 2012). Hence, in the past, bumble bees were likely pervasive across the extent of this relatively small island (27.5 km in length and 1.6 km at its narrowest point) as they are in the present day. Based on the overall evenness of the communities sampled in 2018, spatial autocorrelation is not likely to have been a significant source of bias in historical collection efforts, further justifying individual-based rarefaction as an approach to comparing historical and contemporary species occurrence data in this study. With that said, historical collections are biased toward the north end of the island, and the occurrence of singletons suggests possible unevenness in the distribution of the historical fauna. Differences in habitat diversity between the north and south ends of Galiano Island (with more modified rural environs, open woodlands, and rock outcrops toward the south end) could have resulted in a biased picture of the historical community, especially with respect to species having narrow habitat requirements, such as *B. fervidus*.

In this study, the historical bumble bee sample size is small ($n = 278$). Our estimation of species

decline should thus be considered a minimum estimate, as other species may well have occurred on the island in the past. Additionally, while three of the undetected species occurred in relatively large numbers historically, two species (*B. fervidus* and *B. flavidus*) are represented by singletons in the historical record. These singletons may represent small historical populations that have since disappeared, or vagrants that never successfully established on the island. The cuckoo bumble bee *B. flavidus* is a widespread holarctic species (Lhomme et al. 2021), demonstrating a high potential for dispersal. *Bombus fervidus*, on the other hand, has a range limited to North America, where it has shown a poorly understood but consistent pattern of decline in relative abundance since 1990 (Hatfield et al. 2015b). In this case, given its habitat preferences (open grassland, old fields, and tallgrass habitats), it may have struggled to get established on this forested island. Yet it is also possible that certain habitats (e.g., rural areas) were undersampled in the past, where *B. fervidus* may have been well established.

The disappearance of *B. occidentalis* along with the cuckoo bumble bees *B. insularis* and *B. suckleyi* is interesting to note in light of known parasitic relationships between these species (Thorp et al. 1983, Williams et al. 2014). Yet while *B. insularis* is a versatile parasite associated with multiple species in the local fauna, several of which persist today, *B. suckleyi* is not known to associate with any species reported for the island other than *B. occidentalis*. *Bombus suckleyi* thus appears to have vanished as an obligate parasite along with its host, consistent with trends elsewhere (Hatfield et al. 2015a, COSEWIC 2019). *Bombus suckleyi* has not been detected in British Columbia since 2013, despite extensive surveys, though it may persist in northern parts of the province where surveys have been less intensive (COSEWIC 2019).

Parasitic associations among the Galiano Island bumble bee fauna could have also resulted in higher rates of infection by *Vairimorpha bombi*, compounding the stressors afflicting these species. Four out of the five species reported extirpated from Galiano Island (*B. fervidus*, *B. flavidus*,

B. occidentalis, *B. suckleyi*) are frequently infected by *V. bombi* (Gillespie 2010, Cameron et al. 2011, Lozier et al. 2011, Cordes et al. 2012, Pampell et al. 2015, McArt et al. 2017). Parasitic interactions among cuckoo bumble bees and their hosts could result in pathogen spillover involving *V. bombi*, which here may have contributed to their mutual demise. More work is necessary to evaluate the threat of pathogens such as *V. bombi*, as some bumble bee populations have demonstrated high pathogen prevalence yet no indication of decline (Koch and Strange 2012).

Other potential sources of environmental stress on Galiano Island historically include apiculture, logging, and reforestation, the last of which may have resulted in the loss of habitat for some bumble bees. Indeed, logging and subsequent reforestation represents the most significant landscape change that has occurred on Galiano Island over the last half century (MES 2008, 2017). Disturbance events such as forest fire and clearcuts can potentially create habitat for pollinators (Hanula et al. 2015, Korpela et al. 2015, Ponisio et al. 2016, Roberts et al. 2017, Mola and Williams 2018); subsequent forest succession may then result in declining bee biodiversity (Rivers and Betts 2021). That said, the importance of forests has largely been overlooked to date in terms of the resources they provide for bumble bees (Mola et al. 2021). The implications of forest succession for bumble bee population dynamics thus remain poorly understood.

Given the limited extent of agriculture on the island, pesticide use is not likely an important factor contributing to this case of bumble bee extirpation. Other potential stressors include the effects of bumble bee sex determination on genetic diversity at low population sizes (Zayed and Packer 2005, Lozier et al. 2011). Due to its proximity to other land masses, however, Galiano Island is not a strictly insular system, remaining subject to periodic migration or colonization by outside populations. Indeed, local Indigenous knowledge indicates that long-distance dispersal of bumble bees does occur in this archipelago. According to Rosemary Georgeson, an Indigenous resident of Galiano Island, a large bumble bee was once observed flying across the Salish Sea, landing

on her boar near the mouth of the Fraser River (Rosemary Georgeson, personal communication; see supplemental material). The details of this account, including the size of the bumble bee, the time of year, and apparent distance traveled, are consistent with the long-range dispersal of a new queen.

Colonization: The Arrival of *Bombus vosnesenskii*

Bombus vosnesenskii was first observed on Galiano Island in 2017 and subsequently collected using blue vane traps, marking another historical change in the local fauna. Shifts in bumble bee community composition may be expected to occur in the wake of local extinction (extirpation) events, as in the case of *B. vosnesenskii*'s recent range expansion following the decline of *B. occidentalis* (Fraser et al. 2012). *Bombus vosnesenskii* has become dominant in many urban environments (McFrederick and LeBuhn 2006, Cole et al. 2019), though we found it occurred relatively infrequently on Galiano Island (Table 3). Researchers have previously suggested a threshold of urbanization that must be crossed before *B. vosnesenskii* assumes prominence in a community (McFrederick and LeBuhn 2006). Thus, this species may be struggling to establish on this largely forested island. On the other hand, *B. vosnesenskii*'s low abundance may simply be the result of its recent colonization of Galiano Island.

Potential interactions between *B. vosnesenskii* and *B. sitkensis* were also noted in this study. We found *B. sitkensis* to be least abundant in dry modified habitats where *B. vosnesenskii* was most prevalent; conversely, *B. sitkensis* was most abundant in wetland habitats where *B. vosnesenskii* was least common. These findings are consistent with previous research citing the negative influence of *B. vosnesenskii* on bumble bee community richness in urban environments, where populations of *B. sitkensis* have been found to be particularly negatively affected (McFrederick and LeBuhn 2006, Cole et al. 2019). Researchers have postulated that this effect may be due to competitive exclusion; both *B. sitkensis* and *B. vosnesenskii* are subterranean nesters, making them potential

competitors for nesting habitat (McFrederick and LeBuhn 2006). However, the significant habitat differences that we detected for these species could simply indicate a preference for wetlands on the part of *B. sitkensis* and for disturbed environments on the part of *B. vosnesenskii*. From this perspective, our results indicate that the effect of competitive exclusion previously reported for these species could be confounded by, coincide with, or be mitigated by niche segregation. Further research is required to understand interactions between these species given the recent arrival of *B. vosnesenskii* on Galiano Island.

Conclusion

Baseline data are rare for many insect groups, including bumble bees, making population analysis difficult (MacPhail et al. 2019). As a result, important pollinator species may undergo dramatic declines unnoticed (Buchmann and Nabhan 1996). Our study demonstrates the efficacy of two forms of search effort in detecting ecological change in a bumble bee community with reference to a historical baseline dataset comprising 278 museum specimens. Rarefaction curves generated from intensive blue vane sampling and iNaturalist observations converged on the same estimate of bumble bee species richness. Comparison of both sources of contemporary species occurrence data against historical data enabled the detection of changes in community composition, though as a caveat it should be noted that the local species pool (maximum of 10 species) and study area (57 km²) were small.

Blue vane traps are optimal for sampling large insects such as bumble bees (Stephen and Rao 2005), yet as the results of this study demonstrate, they can also result in high mortality. This mortality is of particular concern with respect to social insects such as bumble bees, for which passive sampling of queens during the early spring period could negatively affect populations (Gezon et al. 2015, Gibbs et al. 2017). Our findings demonstrate that bumble bee surveys need not necessarily be so intensive, however, depending on research goals, as well as the size of the species pool and the area under

study. Further research deploying alternative sampling methods alongside blue vane traps and iNaturalist is necessary to compare their efficacy in estimating species diversity, richness, and evenness in bumble bee communities. Developing a non-lethal methodology for reliably surveying bumble bee communities is critical to promote more sustainable and compassionate wildlife research practices in the future (Tepedino and Portman 2020, Zemanova 2020).

In this study, iNaturalist observations crowdsourced over the timespan of 5 years produced a reliable estimate of species richness, comparable to estimates obtained through intensive sampling using blue vane traps. These results indicate that iNaturalist might be harnessed to detect changes in the composition of ecological communities in limited cases where: a) adequate historical baseline data are available; b) the study area and local species pool of the target taxonomic group is relatively small; and c) there is low spatial autocorrelation of species occurrences. Collection of physical specimens may still be required to validate difficult taxa such as *Bombus vosnesenskii*, which requires careful examination to discriminate from *B. caliginosus* (Williams et al. 2014). Further inventory work combining methods to sample bumble bees on different spatial scales is warranted to determine the reliability of community science data for monitoring ecological change.

Acknowledgments

We thank the BC Parks Living Lab program, the Ian McTaggart Cowan Professorship in the School of Environmental Studies at the University of Victoria, and the Natural Sciences and Engineering Research Council of Canada for funding this research. We are likewise grateful to Pascale Archibald, Sarah Johnson, Daniel Kirkpatrick, Kevin Toomer, and Marika van Reeuyk, who supported field work and aided with the processing and identification of bumble bees. Thank you to Claudia Copley, Joel Gibson, and Karen Needham for facilitating access to specimens at the Royal British Columbia Museum and UBC Beaty Biodiversity Museum. Our thanks

to John Ascher who tirelessly identifies bees on iNaturalist, and to Trevor Lantz who provided valuable feedback on early analyses and drafts. We also thank the following organizations who provided access to the sites necessary to conduct this research: BC Parks, Crystal Mountain Society, Islands Trust Conservancy, Galiano

Club, Galiano Conservancy Association, Galiano Island Parks and Recreation Commission, Garry Oak Meadow Preservation Society, and Tapovan Sri Chinmoy Peace Park. Finally, we thank the many Galiano Island community members who permitted sampling on private land, and who otherwise supported this work.

Literature Cited

- Antonovics, J., and M. Edwards. 2011. Spatio-temporal dynamics of bumblebee nest parasites (*Bombus* subgenus *Psythirus* spp.) and their hosts (*Bombus* spp.). *Journal of Animal Ecology* 80:999-1011.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67:1-48. Available online at <https://doi.org/10.18637/jss.v067.i01> (accessed 19 September 2023).
- Biella, P., G. Bogliani, M. Cornalba, A. Manino, J. Neumayer, M. Porporato, P. Rasmont, and P. Milanesi. 2017. Distribution patterns of the cold adapted bumblebee *Bombus alpinus* in the Alps and hints of an uphill shift (Insecta: Hymenoptera: Apidae). *Journal of Insect Conservation* 21:357-366.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9(2):378-400. Available online at <https://doi.org/10.32614/RJ-2017-066> (accessed 19 September 2023).
- Buchanan, A., J. Gibbs, L. Komondy, and Z. Szendrei. 2017. Bee community of commercial potato fields in Michigan and *Bombus impatiens* visitation to neonicotinoid-treated potato plants. *Insects* 8:30.
- Buchmann, S. L., and G. P. Nabhan. 1996. *The Forgotten Pollinators*. Island Press, Washington, DC.
- Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences (USA)* 108:662-667.
- Cayuela, L. and N. J. Gotelli. 2014. rareNMtests: ecological and biogeographical null model tests for comparing rarefaction curves. R package version 1.1. Available online at <https://cran.r-project.org/web/packages/rareNMtests/rareNMtests.pdf> (accessed 19 September 2023).
- Cayuela, L., N. J. Gotelli, and R. K. Colwell. 2015. Ecological and biogeographic null hypotheses for comparing rarefaction curves. *Ecological Monographs* 85:437-455.
- Chao, A. 1984. Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11:265-270.
- Colla, S. R., and C. M. Ratti. 2010. Evidence for the decline of the western bumble bee (*Bombus occidentalis* Greene) in British Columbia. *The Pan-Pacific Entomologist* 86:32-34.
- Cole, J. S., R. B. Siegel, H. L. Loffland, M. W. Tingley, E. A. Elsey, and M. Johnson. 2019. Explaining the birds and the bees: deriving habitat restoration targets from multi-species occupancy models. *Ecosphere* 10:e02718.
- Cordes, N., W. Huang, J. P. Strange, S. A. Cameron, T. L. Griswold, J. D. Lozier, and L. F. Solter. 2012. Interspecific geographic distribution and variation of the pathogens *Nosema bombi* and *Crithidia* species in United States bumble bee populations. *Journal of Invertebrate Pathology* 109:209-216.
- [COSEWIC] Committee on the Status of Endangered Wildlife in Canada. 2014. COSEWIC assessment and status report on the Western Bumble Bee, *Bombus occidentalis*, *occidentalis* subspecies - *Bombus occidentalis occidentalis*, *mckayi* subspecies - *Bombus occidentalis mckayi*, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON. Available online at https://wildlife-species.canada.ca/species-risk-registry/virtual_sara/files/cosewic/sr_Western%20Bumble%20Bee_2014_e.pdf (accessed 28 May 2022).
- [COSEWIC] Committee on the Status of Endangered Wildlife in Canada. 2019. COSEWIC assessment and status report on the Suckleyi's Cuckoo Bumble Bee *Bombus suckleyi* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON. Available online at https://wildlife-species.canada.ca/species-risk-registry/virtual_sara/files/cosewic/sr%2DBourdonSuckleysCuckooBumbleBee%2Dv00%2D2020Oct%2DEng1%2Epdf (accessed 28 May 2022).
- Dryad. 2023. Available online at <https://doi.org/10.5061/dryad.59zw3r2b3> (accessed 19 September 2023).

- Emmings, K., and K. Erickson. 2004. Galiano Island Landscape Classification and UP-CLOSE Workshop Series Final Report. Galiano Island, BC. Available online at https://galianoconservancy.ca/wp-content/uploads/2016/11/final_report_complete.pdf (accessed 15 August 2022).
- Fraser, D., C. Copley, E. Elle, and R. Cannings. 2012. Changes in the status and distribution of the yellow-faced bumble bee. *Journal of the Entomological Society of British Columbia* 109:31-37.
- Geroff, R. K., J. Gibbs, and K. W. McCravy. 2014. Assessing bee (Hymenoptera: Apoidea) diversity of an Illinois restored tallgrass prairie: methodology and conservation considerations. *Journal of Insect Conservation* 18:951-964.
- Gezon, Z. J., S. Wyman, J. S. Ascher, D. W. Inouye, and R. E. Irwin. 2015. The effect of repeated, lethal sampling on wild bee abundance and diversity. *Methods in Ecology & Evolution* 6:1044-1054.
- Gibbs, J., N. K. Joshi, J. K. Wilson, N. L. Rothwell, K. Powers, M. Haas, L. Gut, D. J. Biddinger, and R. Isaacs. 2017. Does passive sampling accurately reflect the bee (Apoidea: Anthophila) communities pollinating apple and sour cherry orchards? *Environmental Entomology* 46:579-588.
- Gillespie, S. 2010. Factors affecting parasite prevalence among wild bumblebees. *Ecological Entomology* 35:737-747.
- Graystock, P., E. J. Blane, Q. S. McFrederick, D. Goulson, and W. Hughes. 2016. Do managed bees drive parasite spread and emergence in wild bees? *International Journal for Parasitology: Parasites and Wildlife* 5:64-75.
- Grupe, A. C., and C. A. Quandt. 2020. A growing pandemic: a review of *Nosema* parasites in globally distributed domesticated and native bees. *PLoS Pathogens* 16:e1008580.
- Guzman, L. M., S. A. Johnson, A. O. Mooers, and L. K. M'Gonigle. 2021. Using historical data to estimate bumble bee occurrence: variable trends across species provide little support for community-level declines. *Biological Conservation* 257:109141.
- Hanula, J. L., S. Horn, and J. J. O'Brien. 2015. Have changing conditions contributed to pollinator decline in the southeastern United States? *Forest Ecology and Management* 348:142-152.
- Hatfield, R., S. Jepsen, R. Thorp, L. Richardson, and S. Colla. 2015a. *Bombus suckleyi*. The IUCN Red List of Threatened Species 2015: e.T44937699A46440241. International Union for Conservation of Nature, Gland, Switzerland. Available online at <http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T44937699A46440241.en> (accessed 10 December 2021).
- Hatfield, R., S. Jepsen, R. Thorp, L. Richardson, S. Colla, and S. Foltz Jordan. 2015b. *Bombus fervidus*. The IUCN Red List of Threatened Species 2015: e.T21215132A21215225. International Union for Conservation of Nature, Gland, Switzerland. Available online at: <http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T21215132A21215225.en> (accessed 10 December 2021).
- iNaturalist. 2017. Available online at <https://www.inaturalist.org/observations/6412054> (accessed 01 January 2022).
- iNaturalist. 2022. Available online at <https://inaturalist.ca> (accessed 01 January 2022).
- [IUCN] International Union for Conservation of Nature. 2012. IUCN Red List Categories and Criteria: Version 3.1. Second ed. International Union for the Conservation of Nature. Gland and Cambridge, UK. Available online at <https://www.iucn.org/content/iucn-red-list-categories-and-criteria-version-31-second-edition> (accessed 28 May 2022).
- [ITC] Islands Trust Conservancy. 2018. Report: Regional Conservation Plan 2018–2027. Islands Trust Conservancy. Victoria, BC. Available online at https://islandstrust.bc.ca/wp-content/uploads/2020/05/itc_2018-11_rcp-2018-2027-web_fina.pdf (accessed 28 May 2022).
- Kerr, J., T. Jeremy, A. Pindar, P. Galpern, L. Packer, S. G. Potts, S. M. Roberts, P. Rasmont, O. Schweiger, S. R. Colla, L. L. Richardson, and D. L. Wagner. 2015. Climate change impacts on bumblebees converge across continents. *Science* 349:177-180.
- Kimoto, C., S. J. DeBano, R. W. Thorp, S. Rao, W. P. Stephen, and R. Jeanne. 2012. Investigating temporal patterns of a native bee community in a remnant North American bunchgrass prairie using blue vane traps. *Journal of Insect Science* 12:108.
- Klassen, H., S. C. Saunders, K. Kranabetter, A. MacKinnon, H. Griesbauer, and O. Fitzpatrick. 2015. Establishment of an interdisciplinary project to evaluate ecological implications of climate change in dry south coast forest ecosystems. Technical Report 086. Ministry of Forests, Lands and Natural Resource Operations, Nanaimo, BC.
- Koch, J. B., and J. P. Strange. 2012. The status of *Bombus occidentalis* and *B. moderatus* in Alaska with special focus on *Nosema bombi* incidence. *Northwest Science*. 86:212-220.
- Korpela, E.-L., T. Hyvonen, and M. Kuussaari. 2015. Logging in boreal field-forest ecotones promotes flower-visiting insect diversity and modified insect community composition. *Insect Conservation and Diversity* 8:152-162.
- Lhomme, P., S. D. Williams, G. Ghisbain, B. Martinet, M. Gérard, and H. M. Hines. 2021. Diversification pattern of the widespread Holarctic cuckoo bumble bee, *Bombus flavidus* (Hymenoptera: Apidae): the east side story. *Insect Systematics and Diversity* 5:5.

- Lozier, J. D., J. P. Strange, I. J. Stewart, and S. A. Cameron. 2011. Patterns of range-wide genetic variation in six North American bumble bee (Apidae: *Bombus*) species. *Molecular Ecology* 20:4870-4888.
- MacPhail, V. J., L. L. Richardson, and S. R. Colla. 2019. Incorporating citizen science, museum specimens, and field work into the assessment of extinction risk of the American Bumble bee (*Bombus pensylvanicus* De Geer 1773) in Canada. *Journal of Insect Conservation* 23:597-611.
- [MES] Madrone Environmental Services Ltd. 2008. Terrestrial Ecosystem Mapping of the Coastal Douglas-Fir Biogeoclimatic Zone. Dossier 07.0359. Ministry of Forests Integrated Land Management Bureau, Nanaimo, BC. Available online at <https://a100.gov.bc.ca/pub/acat/public/viewReport.do?reportId=15273> (accessed 10 December 2021).
- [MES] Madrone Environmental Services Ltd. 2017. TEM/SEM mapping updates and disturbance mapping in the Islands Trust Area (Dossier 07.0040). Madrone Environmental Services Ltd., Duncan, BC. Available online at https://islandstrust.bc.ca/wp-content/uploads/2021/04/ITF_2017-09-12_RPT_TEM-SEM-and-Disturbance_FNL.pdf (accessed 28 May 2022).
- McArt, S. H., C. Urbanowicz, S. McCoshum, R. E. Irwin, and L. S. Adler. 2017. Landscape predictors of pathogen prevalence and range contractions in US bumblebees. *Proceedings of the Royal Society B* 284:20172181.
- McCrary, K. W., and J. D. Ruhoff. 2017. Bee (Hymenoptera: Apoidea) diversity and sampling methodology in a Midwestern USA deciduous forest. *Insect* 8:81.
- McFrederick, Q. S., and G. LeBuhn. 2006. Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? *Biological Conservation* 129:372-382.
- Mola, J. M., J. Hemberger, J. Kochanski, L. L. Richardson, and I. S. Pearse. 2021. The importance of forests in bumble bee biology and conservation. *BioScience* 71:1234-1248.
- Mola, J. M., and N. M. Williams. 2018. Fire-induced change in floral abundance, density, and phenology benefits bumble bee foragers. *Ecosphere* 9:e02056.
- Moore, R. D., D. L. Spittlehouse, P. H. Whitfield, and K. Stahl. 2010. Weather and climate. *In* R. G. Pike, T. E. Redding, R. D. Moore, R. D. Winkler, and K. D. Bladon (editors), *Compendium of Forest Hydrology and Geomorphology in British Columbia*, Land Management Handbook, Ministry of Forests and Range, Victoria, BC. Pp. 47-83.
- Nuszdorfer, F. C., K. Klinka, and D. A. Demarchi. 1991. Coastal Douglas-fir zone. *In* D. V. Meidinger and J. Pojar (editors), *Ecosystems of British Columbia*, Ministry of Forests Research Branch, Smithers, BC. Pp. 81-93.
- Oksanen, J. F., B. Guillaume, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'hara, G. L. Simpson, and P. Solymos. 2019. *Vegan: Community ecology package*. R package version 2.5-5. Available online at <https://cran.r-project.org/web/packages/vegan/vegan.pdf> (accessed 19 September 2023).
- Osazuwa-Peters, O. L., W. D. Stevens, and I. Jiménez. 2018. Using museum specimens to estimate broad-scale species richness: exploring the performance of individual-based and spatially explicit rarefaction. *PLOS One* 13:e0204484.
- Osborne, J. L., A. P. Martin, N. L. Carreck, J. L. Swain, M. E. Knight, D. Goulson, R. J. Hale, and R. A. Sanderson. 2008. Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology* 77:406-415.
- Otterstatter, M. C., and J. D. Thomson. 2008. Does pathogen spillover from commercially reared bumble bees threaten wild pollinators? *PLOS One* 3:e2771.
- Pampell, R., D. Sikes, A. Pantoja, P. Holloway, C. Knight, and R. Ranft. 2015. Bumble bees (Hymenoptera: Apidae: *Bombus* spp.) of Interior Alaska: species composition, distribution, seasonal biology, and parasites. *Biodiversity Data Journal*:e5085.
- Ponisio, L. C., K. Wilkin, L. K. M'Gonigle, K. Kulhanek, L. Cook, R. Thorp, T. Griswold, and C. Kremen. 2016. Pyrodiversity begets plant-pollinator community diversity. *Global Change Biology* 22:1794-1808.
- Rao, S., and W. P. Stephen. 2007. *Bombus (Bombus) occidentalis* (Hymenoptera: Apiformes): in decline or recovery. *The Pan-Pacific Entomologist* 83:360-62.
- Rao, S., and J. P. Strange. 2012. Bumble bee (Hymenoptera: Apidae) foraging distance and colony density associated with a late-season mass flowering crop. *Environmental Entomology* 41:905-915.
- R Core Team. 2019. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rhoades, P., T. Griswold, L. Waits, N. A. Bosque-Pérez, C. M. Kennedy, and S. D. Eigenbrode. 2017. Sampling technique affects detection of habitat factors influencing wild bee communities. *Journal of Insect Conservation* 21:703-714.
- Rhoades, P. R., J. B. Koch, L. P. Waits, J. P. Strange, and S. D. Eigenbrode. 2016. Evidence for *Bombus occidentalis* (Hymenoptera: Apidae) populations in the Olympic Peninsula, the Palouse Prairie, and forests of northern Idaho. *Journal of Insect Science* 16:20.
- Rivers, J. W., and M. G. Betts. 2021. Postharvest bee diversity is high but declines rapidly with stand age in regenerating Douglas-fir forest. *Forest Science* 67:275-285.

- Rivers, J. W., C. L. Mathis, A. R. Moldenke, and M. G. Betts. 2018. Wild bee diversity is enhanced by experimental removal of timber harvest residue within intensively managed conifer forest. *GCB Bioenergy* 10:766-781.
- Roberts, H. P., D. I. King, and J. Milam. 2017. Factors affecting bee communities in forest openings and adjacent mature forest. *Forest Ecology and Management* 394:111-122.
- Sanchez-Bayo, F., and K. Goka. 2014. Pesticide residues and bees—a risk assessment. *PLOS One* 9:e94482.
- Shackelford, N., R. J. Standish, W. Ripple, and B. M. Starzomski. 2018. Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. *Conservation Biology* 32:672-684.
- Simon, A. D. F., H. E. Marx, and B. M. Starzomski. 2021. Phylogenetic restriction of plant invasion in drought-stressed environments: implications for insect-pollinated plant communities in water-limited ecosystems. *Ecology and Evolution* 11:10042-10053.
- Stephen, W. P., and S. Rao. 2005. Unscented traps for non-*Apis* bees (Hymenoptera: Apoidea). *Journal of the Kansas Entomological Society* 78:373-380.
- Stephen, W. P., and S. Rao. 2007. Sampling native bees in proximity to a highly competitive food resource (Hymenoptera: Apiformes). *Journal of the Kansas Entomological Society* 80:369-376.
- Szabo, N. D., S. R. Colla, D. L. Wagner, L. F. Gall, and J. T. Kerr. 2012. Do pathogen spillover, pesticide use, or habitat loss explain recent North American bumblebee declines? *Conservation Letters* 5:232-239.
- Tepedino V. J., and Z. M. Portman. 2020. Intensive monitoring for bees in North America: indispensable or improvident? *Insect Conservation and Diversity* 14:535-542.
- Thorp, R. W., D. S. Horning, and L. L. Dunning. 1983. *Bumble bees and cuckoo bumble bees of California* (Hymenoptera: Apidae) Vol. 23. University of California Press, Berkeley.
- Tokarev, Y. S., W. F. Huang, L. F. Solter, J. M. Malysch, J. J. Becnel, and C. R. Vossbrinck. 2020. A formal redefinition of the genera *Nosema* and *Vairimorpha* (Microsporidia: Nosematidae) and reassignment of species based on molecular phylogenetics. *Journal of Invertebrate Pathology* 169:107279.
- Vavrek, M. J. 2011. Fossil: palaeoecological and palaeogeographical analysis tools. *Palaeontologia Electronica* 14:1T.
- Wilson, J. S., T. Griswold, and O. J. Messinger. 2008. Sampling bee communities (Hymenoptera: Apiformes) in a desert landscape: are pan traps sufficient? *Journal of the Kansas Entomological Society* 81:288-300.
- Williams, P. H., R. W. Thorp, L. L. Richardson, and S. R. Colla. 2014. *Bumble Bees of North America: An Identification Guide*. Princeton University Press, Princeton, NJ.
- Zayed, A., and L. Packer. 2005. Complementary sex determination substantially increases extinction proneness of haplodiploid populations. *Proceedings of the National Academy of Sciences of the United States of America* 102:10742-10746.
- Zemanova, M. A. 2020. Towards more compassionate wildlife research through the 3Rs principles: moving from invasive to non-invasive methods. *Wildlife Biology* 2020:1-17.

Supplemental material available online at <http://www.bioone.org/loi/nwsc>

Submitted 20 December 2021

Accepted 16 September 2022