Multiple measures of biodiversity change make for the strongest analyses with historical data – Reply to Guzman et al. 2021

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Guzman et al.'s (2021) comment on occupancy models from Soroye et al. (2020) explores parameterization with a series of simulations and concludes that modelled rates of bumblebee decline in North America were overestimated. We welcome this foray into occupancy modelling approaches. Yet, Guzman et al. (2021) missed the key messages from our work with their dismissal of bumblebee declines based on their choices of occupancy modelling approach, while underestimating species declines known from independent data sources. Theirs is a recipe for justifying conservation inaction despite multiple lines of evidence that many species are threatened or soon will be.

In Soroye et al. (2020), we used a large dataset of historic North American and European bumblebee observations to link recent species- and assemblage-level change to climate change, having created a new method to identify the frequency and severity of extreme weather relative to species' realized niche limits. We supported discoveries with multiple, robust tests of historic change in assemblage richness, observed extirpation, observed colonization, and change in probability of occupancy, while accounting for variation in sampling effort in various ways. While we presented continental estimates of observed declines, we discovered relationships between biodiversity change and climate change. We did not present species-level estimates of change or endangerment. As Guzman et al. (2021) note, conservation practitioners require accurate estimates of species decline for listing species for protection. This process of estimating absolute levels of population change must be rigorous, including expert insight and independent tests of recent and historic change (e.g. IUCN Red List), something we did not attempt and that Guzman et al. (2021) should not have attempted in isolation from detailed, species-specific knowledge.

Instead, Guzman et al. (2021) conclude from occupancy models that there is little evidence of widespread declines in bumblebees, despite the fact that declines in North American and European bumblebees have been observed in detail over recent decades (e.g. (Goulson et al. 2008; Kerr et al. 2015)). The IUCN Red List indicates that 8 of 33 North American species in our study (24%) face different levels of endangerment and are listed as "decreasing". Yet, quantitative analysis in those expert assessments also indicate that about 51% of species (17/33) may have experienced decline over recent decades (Table 1). Comparing occupancy results from both Soroye et al. (2020) and Guzman et al. (2021) to these expert assessments (Table 1) suggests that while Soroye et al. (2020) overestimate declines, Guzman et al. (2021) underestimate them by a similar margin (for species for which measurements exist). Guzman et al.'s models show an increasing occupancy trend for five species with expert-assessed average declines. Occupancy models should not be used to predict declines without validation against independent sources, like IUCN Red List assessments.

Precise knowledge of population trends is missing for many species, which underscores the vital need for expert estimates of population change to ground pure modelling results of the sort advocated by Guzman et al. While IUCN Red List assessments for North American species provide detailed quantitative information on population declines and species trends (e.g. Table 1), no such information is available for European Red List assessments, even for threatened species (e.g. (Rasmont et al. 2015)).

In focusing on the occupancy modelling methods of our original paper, Guzman et al. (2021) ignore the key discoveries in that work and the multiple lines of evidence that support them. Importantly, they find that occupancy estimates in Europe appear robust to changes in model parameterization, further supporting the interpretation of our results there (aside from estimates of uncertainty). Guzman et al. (2021) also incorrectly state that we removed *Bombus distinguendus* from analyses. As noted in Soroye et al. (2020), *B. distinguendus* was omitted from calculations of continental change in North America because it was not observed in the historic period. This species was retained otherwise.

Occupancy modelling offers a useful way to understand biodiversity change, but given the observed sensitivity of occupancy models to differences in model parameterization and rapidly evolving modelling techniques, large-scale studies of biodiversity change with historic data should focus on measuring change in multiple ways (i.e. not just with occupancy models) and comparing model results to independently generated estimates. Proposing and testing "risky predictions" (after Karl Popper) with multiple, independent lines of evidence (e.g. from species richness change, observed extinction, observed colonization), and accounting for sampling in various ways (e.g. measuring richness change in well-sampled areas, using sampling as a covariate in models, testing various thresholds for inferred absence of a species, testing multiple spatial resolutions of analysis, using occupancy models) allows for robust tests of theory that can reveal potential cross-continental mechanisms of decline, as done in Soroye et al. (2020). Approaches like this, which use occupancy models as one among many tools, provide far stronger bases for proposing and testing mechanisms of global change-related biodiversity change.

Acknowledgements

References

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Table 1. Species-specific estimates of decline compared to independently assessed estimates of average decline as reported in species' IUCN Red List assessments. No European species had detailed information provided, and 16 North American species with an average decline of zero were excluded (this typically indicated suspected stable or increasing population trend). Details are all from global assessments, except for *B. bohemicus* (which occurs in Europe as well) where we used the North American-specific details provided in the assessment.

Species	IUCN status	IUCN population trend	IUCN average decline	Guzman et al occupancy change	Soroye et al occupancy change	Guzman et al difference	Soroye et al difference
affinis	CR	decreasing	-69.36	-69.00	-83.72	0.36	-14.36
appositus	LC	unknown	-28.40	8.74	-45.79	37.14	-17.39
auricomus	LC	stable	-24.11	0.81	-47.59	24.92	-23.48
bohemicus	CR	decreasing	-94.77	-72.58	-27.07	22.19	67.70
borealis	LC	stable	-7.11	-42.05	-68.22	-34.94	-61.11
centralis	LC	stable	-7.55	16.42	-42.63	23.97	-35.08
fervidus	VU	decreasing	-30.69	-1.89	-40.86	28.80	-10.17
fraternus	EN	decreasing	-59.96	-42.30	-68.59	17.66	-8.63
huntii	LC	stable	-25.34	-8.11	-56.45	17.23	-31.11
insularis	LC	stable	-12.37	-12.68	-56.28	-0.31	-43.91
melanopygus	LC	stable	-15.78	13.51	-44.88	29.29	-29.10
morrisoni	VU	decreasing	-57.74	-50.81	-74.07	6.93	-16.33
nevadensis	LC	stable	-15.48	3.81	-52.35	19.29	-36.87
occidentalis	VU	decreasing	-40.32	-20.62	-53.19	19.70	-12.87
pensylvanicus	VU	decreasing	-51.38	-44.30	-65.77	7.08	-14.39
sylvicola	LC	stable	-10.23	-1.52	-55.52	8.71	-45.29
terricola	VU	decreasing	-49.94	-38.95	-66.10	10.99	-16.16
		Mean (±SE)	-35.32 (5.91)	-21.26 (6.75)	-55.83 (3.31)	14.06 (3.85)	-20.50 (6.36)
		Median	-28.40	-12.68	-55.52	17.66	-17.39