Title

Potential host number in cuckoo bees (Psithyrus subgen.) increases toward higher elevations

Permalink

https://escholarship.org/uc/item/78k1383t

Journal

Frontiers of Biogeography, 5(2)

Authors

Pradervand, Jean-Nicolas
Pellissier, Loic
Litsios, Glenn
et al.

Publication Date

2013

DOI

10.21425/F5FBG15994

research letter ISSN 1948-6596

Potential hosts number in cuckoo bees (*Psithyrus* subgenus) increases towards higher elevations

Jean-Nicolas Pradervand[1,*], Loïc Pellissier[2], Glenn Litsios[1,3], Antoine Guisan[1]

[1]Department of Ecology and Evolution, University of Lausanne, Bâtiment Biophore, 1015 Lausanne, Switzerland.

[2] The Arctic Research Centre, Department of Bioscience, Aarhus University, Aarhus, Denmark.

[3]Swiss Institute of Bioinformatics, Quartier Sorge, 1015 Lausanne, Switzerland

[*] jean-nicolas.pradervand@unil.ch

Abstract. In severe and variable conditions, specialized resource selection strategies should be less frequent because extinction risks increase for species that depend on a single and unstable resource. *Psithyrus* (*Bombus* subgenus *Psithyrus*) are bumblebee parasites that usurp *Bombus* nests and display inter-specific variation in the number of hosts they parasitize. Using a phylogenetic comparative framework, we show that *Psithyrus* species at higher elevations display a higher number of hosts species compared with species restricted to lower elevations. Species inhabiting high elevations also cover a larger temperature range, suggesting that species able to occur in colder conditions may benefit from recruitment from populations occurring in warmer conditions. Our results provide evidence for an 'altitudinal niche breadth hypothesis' in parasitic species, showing a decrease in the parasites' specialization along the elevational gradient, and also suggesting that Rapoport's rule might apply to *Psithyrus*.

Keywords. altitude, altitudinal gradient, bee, generalist, geographic range, gradient, niche breadth, parasitism, Rapoport, specialist

Introduction

Optimal resource selection is crucial for all organisms and directly impacts fitness (Parker and Stuart 1976). Among species, resource selection ranges from highly specialized (i.e., small range of resources consumed) to highly generalized (i.e., large range of resources consumed). Furthermore, different resource selection strategies may not generate identical costs and benefits in mild compared to severe environments. Indeed, resource specialization is expected to be more advantageous in stable environments, where fluctuations of resources' availability are low, and intense competition favours niche partitioning (MacArthur 1955). In contrast, more generalist species should be advantaged in severe environments where resources are fluctuating, since they do not depend on a restricted range of resources that may become temporarily unavailable (Currie 1991).

Generally, parasites obtain resources from a host in the form of nutrients (e.g., body fluids), and also habitats (e.g., nest). The latter is particularly widespread in social insects, because nest parasites benefit from the workforce of non-reproductive females after taking over the nest (Wcislo 1987). As host availability and population stability vary along environmental gradients (Brinck 1974), parasites should be more host specialized in more productive and stable environments, compared with severe conditions. Latitude has been traditionally associated with such an environmental gradient, inspiring the 'latitude niche breadth hypothesis' (MacArthur 1972). It may explain, for example, the increased host range exploited by cuckoo birds at higher latitude (Yom-Tov and Geffen 2005). By extending this rule to the geographical range of species, Rapoport suggested that species occupying, on average, higher latitudes should also display a larger latitudinal range (Rapoport 1975). Yet the use of latitude may not represent a stability gradient and is confounded by historical and biogeographical factors (Vázquez and Stevens 2004). For instance, it remains unclear whether the higher frequency of social parasites at higher latitude arises from ecological or historical constraints (Wcislo 1987). To keep away from such biases, one would need to study a geographically restricted zone which encompasses a wide range of environmental conditions.

Elevation clines developing from lowlands to the summits of mountain ranges show similar environmental gradients to that of latitude from the tropics to the poles. High-elevation environments form a series of marginal habitats often characterized by stronger fluctuations in physical factors, more pronounced temporal (daily and seasonal) variability, and also more stressful and stochastic climatic conditions, than in lowland environments (Brinck 1974). Such conditions probably affect species' population dynamics. Indeed, at high elevations, insect populations undergo heavy fluctuations and community structures are less stable (Gutiérrez and Menéndez 1998). This increased stochasticity may have important consequences for the life history of high-elevation insect parasites, but this is not yet known.

Psithyrus (cuckoo-bees) is a monophyletic group within the *Bombus* genus, whose species parasitize nests of other *Bombus* species (Cameron et al. 2007). The *Psithyrus* individual enters the host colony and either adopts the odour of the invaded nest or tries to take over the queen directly after the nest invasion (Goulson 2010). Then it lays eggs and uses the non-reproductive female workers of the invaded colony to raise its progeny (Goulson, 2010). Among *Psithyrus* species the number of hosts can vary (Rasmont 1988), but it is not yet known how this variation is distributed along environmental gradients and whether the number of hosts per species depends on the environmental conditions. Antonovics and Edwards (2011) showed that parasite -free zones exist at the limit of the range of the species. The advantage provided by being generalist (high number of potential hosts) or specialist (low number of potential hosts) may depend on the prevailing environmental conditions, varying along the altitudinal gradient. Following this rationale, we would thus expect to find higher proportions of generalist *Psithyrus* at high elevations, whereas at low elevations specialists should prevail.

Here we studied the link between host specificity and environmental conditions using the subgenus *Psithyrus.* We sampled 149 bumblebee communities along an elevational gradient in the western Swiss Alps. We coupled environmental niche information with data from the literature on host species and tested the following hypotheses:

1) Host species number decreases with temperature and increases with elevation.
2) Species occupying colder conditions also span a larger temperature range, in accordance with Rapoport's rule.

Materials and methods

The study area is located in the western Swiss Alps and covers 700 km², ranging from 1000 m to 3210 m a.s.l. We selected the sampling sites using balanced stratified random sampling, restricted to open meadows and based on elevation, slope and aspect, thus allowing for accurate estimates of species' niche limits along the elevational gradient. From June to September 2009 and 2010, 149 sites of 50 m x 50 m were sampled (Figure 1). We visited each site every three weeks during the most favourable hours for bumblebee activity (10:00–17:00) and in good weather conditions (i.e., little wind, sunny, high temperatures; number of field days = 146). At each site, we used a net to collect every *Bombus* and *Psithyrus* individual we could during a 45-minute search. Identification of specimens took place in the laboratory.

The number of hosts for each *Psithyrus* species in the study area was obtained from the literature (Amiet 1996, Williams 2008) and ranged from one to five host species. These records constitute an accurate list of all host *Bombus* species that are known to be parasitized by each *Psithyrus* species and thus constitute the 'potential host range'. The 'realized host range', i.e., the field record of all the hosts used by *Psithyrus* species at each location, would be more informative. However, *Bombus* nests are cryptic and very difficult to find in the field, making such data almost impossible to record at the scale of our study zone.

As a measure of environmental severity, degree-days were calculated and interpolated using data from meteorological stations, with a digital elevation model at 100 m resolution (for more detail, see Zimmermann and Kienast 1999).

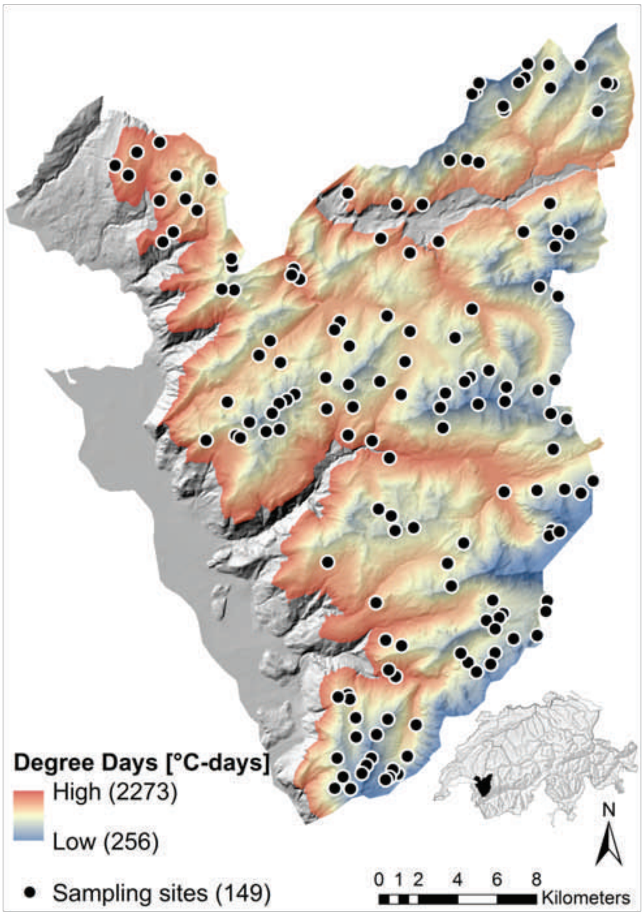

Figure 1. Map of the western Swiss Alps and their location in Switzerland. The coloured area shows the degree-days for all the areas above 1000 m elevation (the lower sampling limit). The black dots represent the sampling sites.

Degree-days are the sum of degrees above 3°C for all days in the year. Decreasing temperature along the elevational gradient is also associated with increased precipitation and climatic variability. In the study area, degree-days are closely related to elevation ($R^2 = 0.98$, $p < 0.001$). The temperature variance increases with elevation (MeteoSwiss data for 187 recording stations in Switzerland, based on the variance of mean daily temperature, $R^2 = 0.23$, $p < 0.001$). As a measure of colder niche edge, we extracted, for each species, the degree-days values for the sites where it occurred and calculated the 20th percentile of those values. We used the 20th percentile instead of the minimum degree-days value to limit the noise of outlier occurrences. We also measured the variance of each species' degree-days values to represent its temperature range. We accounted for species relatedness by using a published phylogeny (Cameron et al. 2007). We related the species-specific host number, the 20th percentile of degree-days and the variance in degree-days using phylogenetic Generalized Least Squares (pGLS), as implemented in the caper R package (Orme et al., 2011). The strength of phylogenetic dependency in our data was accounted for by estimating, using Maximum Likelihood, the λ branch transformation parameter. Other transformations assuming different evolutionary scenarios exist, but they require larger phylogenetic trees to be correctly estimated (R. Freckleton, personal communication). Finally, to show a potential change in the number of *Bombus* species that might affect the availability of hosts to *Psithyrus*, we related the number of *Bombus* species to degree-days using a Generalized Linear Model (GLM) with a quasi-Poisson error distribution.

Results

In the 149 inventoried sites we found eight of the nine *Psithyrus* species (total sampled individuals = 183) occurring in Switzerland and 20 non-parasitic *Bombus* species out of the 31 occurring in Switzerland (total sampled individuals = 1609) (see Table 1 and Figure 1, Pradervand et al. (2011) and Amiet (1996) for more information). We have lumped together three closely related *Bombus* species (*B. terrestis, B. lucorum* and *B. cryptarum*), at the subgenus level (*Bombus sensu stricto*), because of the high probability of wrong identification for this group, especially with old worker bees. The bumblebee species richness is higher at intermediate values of degree-days, corresponding to mid-elevations, and reaches its lowest value in the coldest conditions at high elevation (linear: $t = 4.14$, $DF = 148$, $p < 0.001$, quadratic: $t = -3.91$, $p < 0.001$; Figure 2; see Pellissier *et al.* 2012b for more information). The *Psithyrus* species richness shows a slight linear increase in species richness (linear: $t = 2.56$, $DF = 74$ $p = 0.013$ quadratic: $t= -3.5*10^{-7}$, $p > 0.05$).

Overall, *Psithyrus* individuals are relatively rare, and, while they were found in 49% of our sites, the proportion of *Psithyrus* among bumblebee individuals collected was very low (on average 10% of all observations, consistent with usual proportions of healthy mountain populations; Goulson et al. 2008, Roulston and Goodell 2011). The pGLS regression showed a significant relationship between the species' colder range limit and the number of hosts: *Psithyrus* species tended to have more hosts in cold than in mild conditions ($F = 11.54$; $DF = 2,6$; $p = 0.009$; adjusted $R^2 = 0.60$; $\lambda = 6*10^{-5}$; Figure 3a). Because of the low value of λ we tested whether an Ornstein–Uhlenbeck model of evolution would better fit the data using the Geiger R package, but the Akaike Information Criterion difference was marginal (0.23). Finally, we also found a significant negative correlation between the species colder niche edge and the variance in temperature occupied by the species computed from occurrence data ($F = 7.75$; $DF = 2,6$; $p = 0.022$; adjusted $R^2 = 0.49$; Figure 3b). *Psithyrus* species occurring in colder conditions spanned a larger range of temperature.

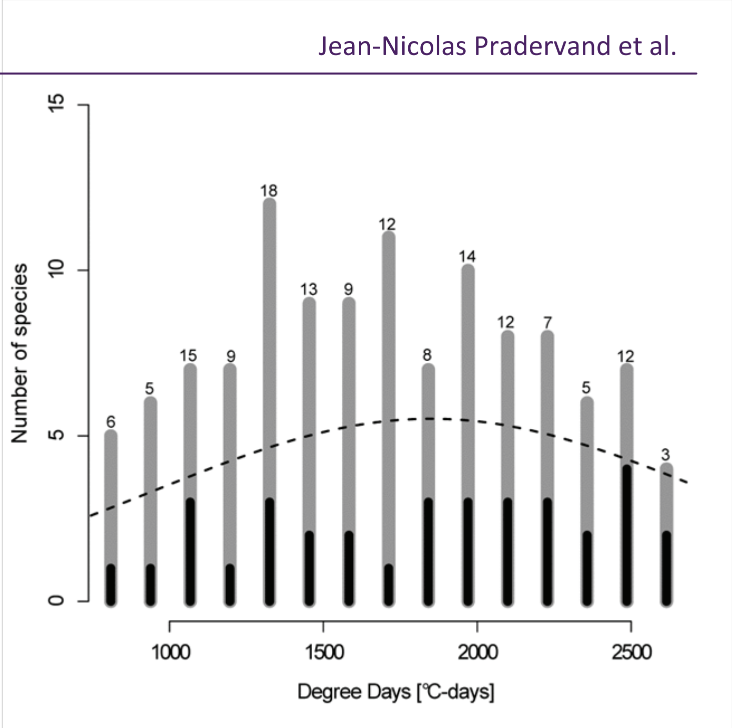

Figure 2. Maximum number of non-parasitic (true bumblebees, in grey) and parasitic (*Psithyrus* subgenus, in black) species in relation to degree-days. The dotted line represents the generalized linear model of the number of non-parasitic species in relation to degree-days. The numbers above the bars indicate the number of sampled communities.

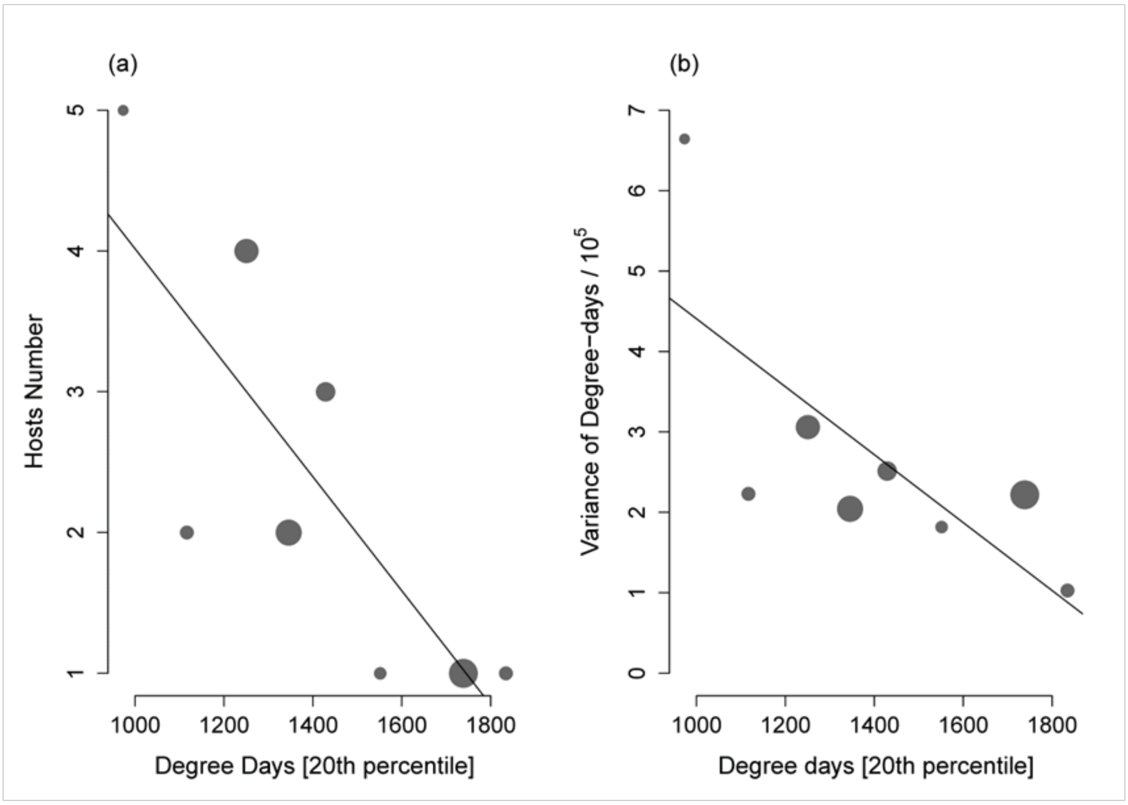

Figure 3. (a) Number of hosts ('Hosts number') for the eight *Psithyrus* species plotted against the colder niche edge (measured as the 20th percentile of their distribution along a gradient of degree-days). The regression line indicates the negative relationship ($R^2 = 0.60$, $p = 0.009$). (b) Variance of degree-days for each species plotted against the colder niche edge. Species with a smaller temperature range tend to occur in warmer conditions ($R^2 = 0.49$, $p = 0.022$). The outlier corresponds to *P. campestris*, which occurs over the whole gradient but is found most in colder conditions. The sizes of the points in both graphs correspond to the number of sites occupied (see Table 1).

Table 1. Prevalence of the *Bombus* and *Psithyrus* species recorded in the study area. The records show the number of individuals recorded. The ‘Plots occupied’ column shows the number of sampling plots occupied by the species. For each species the degree-days (DDEG) and their variance, minimum and 20th percentile are indicated. *Bombus terrestris, B. lucorum* and *B. cryptarum* are amalgamated in the ‘*Bombus s.str.’* subgenus (see main text).

	Presence statistics		Climatic variables				Hosts of the eight *Psithyrus* species							
	Records	Plots occupied	DDEG [°C-days]	varDDEG	minDDEG	20th	*barbutellus*	*bohemicus*	*campestris*	*flavidus*	*norvegicus*	*quadricolor*	*rupestris*	*sylvestris*
B. alpinus	2	2	789.8	40500	744.8	762.8	-	-	-	-	-	-	-	-
B. gerstaeckeri	2	1	1656.7	-	1656.7	1656.7	-	-	-	-	-	-	-	-
B. hortorum	35	28	1859.307	1991016	1047.3	1438.98	R	-	-	-	-	-	-	-
B. humilis	71	39	2055.282	1288370	1341.7	1778.54	-	-	R	-	-	-	-	-
B. hypnorum	13	11	2060.982	1693758	1363.3	1675.5	L	-	-	-	L	-	-	-
B. jonellus	2	1	1363.3	-	1363.3	1363.3	-	-	-	L	-	-	-	L
B. lapidarius	234	76	1803.036	2208483	861.3	1341.7	-	-	-	-	-	-	L	-
B. mendax	44	24	1334.042	1077486	799.3	1045.7	-	-	-	-	-	-	-	-
B. mesomelas	27	23	1571.726	977965.6	1038.5	1342.9	-	-	-	-	-	-	-	-
B. monticola	72	47	1465.9	1768128	744.8	1100.36	-	-	-	L	-	-	-	-
B. mucidus	27	22	1508.973	944057.6	1034.4	1238.42	-	-	-	-	-	-	-	-
B. pascuorum	101	52	2115.075	1141664	1117.4	1910.62	-	-	R	-	-	-	R	-
*B. pomorum**	0	0	-	-	-	-	-	-	R	-	-	-	-	-
B. pratorum	84	57	1772.165	2384115	799.3	1256.88	-	-	L	-	-	-	-	L
B. pyrenaeus	66	37	1275.649	655907.2	799.3	1050.72	-	-	-	-	-	-	-	-
B. ruderarius	50	36	1802.367	1635555	1250.8	1407.1	R	-	R	-	-	-	-	-
B. sicheli	67	39	1501.695	840954.1	969.8	1267.24	-	-	-	-	-	-	L	-
B. soroeensis	279	113	1693.253	2300616	799.3	1261.76	-	-	-	-	-	L/R	-	-
B. subterraneus	3	3	1721.8	457142.7	1558.1	1592.3	-	-	-	-	-	-	-	-
*B. sylvarum**	0	0	-	-	-	-	-	-	-	-	-	-	R	-
B. veteranus	5	5	1871.04	1077605	1513.2	1515.68	-	-	-	-	-	-	-	-
B. wurfleini	135	68	1622.431	1787626	799.3	1296.92	-	-	-	-	-	-	-	-
Bombus s.str.	290	93	1697.26	2485308	799.3	1191.36	-	L	-	-	-	-	-	-
P. barbutellus	12	12	1770.9	2513346	1038.5	1428.94	-	-	-	-	-	-	-	-
P. bohemicus	67	40	2041.2	2220459	1068.8	1738.62	-	-	-	-	-	-	-	-
P. campestris	4	4	1654.075	6645632	868.4	973.34	-	-	-	-	-	-	-	-
P. flavidus	9	7	1424.471	1899382	908.3	1138.36	-	-	-	-	-	-	-	-
P. norvegicus	9	6	2027.5	1029020	1601.7	1834.6	-	-	-	-	-	-	-	-
P. quadricolor	6	5	1910.94	1819100	1350.9	1551.54	-	-	-	-	-	-	-	-
P. rupestris	38	22	1758.236	2792438	799.3	1283.6	-	-	-	-	-	-	-	-
P. sylvestris	38	28	1894.368	2045365	1116.8	1345.42	-	-	-	-	-	-	-	-
Total	1792	-	-	-	-	-	-	-	-	-	-	-	-	-

L = Large elevation variance clade, R= Restricted elevation variance clade according to (Pellissier et al., 2012b), *B. soroeensis* is between the two clades.

* *Bombus sylvarum* and *Bombus pomorum* are two species recorded in the study area but with distributions below 1000m.

Discussion

Host specialization is known to vary between *Psithyrus* species (Rasmont 1988), but it was unknown whether, as for latitudinal gradients, a specialist-to-generalist progression could be found along an elevation cline. In this study we combined environmental data on *Psithyrus* species with their evolutionary history and found that, indeed, species occurring at higher elevation are more generalist than their low-elevation counterparts. The trend was observed despite the decrease of bumblebee species richness at high elevation (Figure 2). Bumblebee species richness follows a hump-shaped pattern typical of a mid-altitudinal diversity peak (Pellissier *et al.* 2012b). Also, we provide evidence of increasing niche breadth with altitude, which parallels the results found for latitude (Krasnov et al. 2008). The fact that generalist *Psithyrus* occurring in the coldest environment also occupy a larger temperature range suggests that Rapoport's rule might also be valid for altitude (Stevens 1992).

Generalist species may be more prevalent in colder environments than specialists because they can compensate for the variation in host populations by parasitizing more species and thus increase the chance of finding a host. Cold and unstable conditions may disadvantage species that are bound to a particular host species. Indeed, it is known that host populations fluctuate more in colder environments (Brinck 1974), making the resources less reliable for specialist parasites. In addition, the length of the vegetation growing season is reduced at high elevations, which constrains the foraging period and thus the time to complete the life cycle (Goulson et al. 2005). This forces *Psithyrus* species emerging at high elevations to quickly find a host to raise their progeny before the end of the nesting season. Being able to colonize any nest encountered is thus likely to be an advantage. Interestingly, generalist species occurring in cold conditions, such as *P. rupestris* and *P. campestris*, lack the specific cuticular carbohydrates that are used as recognition chemicals (Martin et al. 2010), leaving open the possibility of invading a larger number of host species' nests and reducing the search time needed. In contrast, specialist species that mimic the odours of a particular host species probably show a double limitation to their distribution. First, they are associated with host species that are mostly absent in cold environments (Pradervand et al. 2011), and second, environmental constraints of unstable environments may prevent the persistence of populations.

Generalist *Psithyrus* species occurring in the coldest environmental conditions also occupy warmer sites. Among their potential hosts they thus have a range of different species occurring at different elevations. This result parallels the much-discussed Rapoport's rule, which suggests that latitudinal ranges of plants and animals are generally smaller at lower than higher latitudes (Rapoport 1975, Stevens 1992). We found that generalist species occupy a wider temperature range than more specialized species and are therefore likely to encounter more potential host species to parasitize. Paralleling our results, Sanders (2002) found that the elevational range sizes of ants from Colorado, Nevada and Utah widen with increasing elevation. Such patterns following Rapoport's rule may be explained by a rescue effect: unstable populations occurring at high elevations might benefit from constant recruitment from stable populations occurring at lower elevations (Stevens 1992).

In this study, we sampled and analysed the distribution of adult specimens under the assumption that they were caught close to the nest they parasitize. To remove this potential source of bias, one would need to sample the *Psithyrus* directly in the parasitized nest, which is very difficult because they are cryptic and buried deep in the soil. Moreover, invasion can only be confirmed when the offspring leaves the nest because parasites sometimes use the nest as periodic shelter (Rasmont 1988).

In conclusion, we showed that *Psithyrus* species occurring at high elevation tend to parasitize more host species (Figure 3a), suggesting an environmental filtering effect that allows only generalist species to survive in those conditions. Our results not only provide direct support consistent with the altitudinal niche breath hypothesis, but also provide echoing evidence consistent with Rapoport's rule as applied to an altitudinal gradient. Interestingly, generalist species able to occur at higher elevation have a more basal position in the phylogeny, suggesting that the specialized species may have evolved from generalist ancestors. However, this requires further research using a larger *Psithyrus* species sample because incomplete taxon sampling could bias ancestral state reconstruction (Litsios & Salamin 2012). Recent studies are starting to reveal a common pattern for the prevalence of generalist species in more severe conditions at high elevations in trophic and mutualistic interactions, in insects and plants (Pellissier et al. 2012a). Further investigations of other species' interactions and niche breadths along altitudinal gradients are thus required to assess the universality across biotic interactions of the altitudinal niche breadth hypothesis.

Acknowledgments

We thank all the people who helped with the field work. Special thanks to F. Amiet for his help with identifications and S. Litsios for English corrections. We are thankful to J. Beck, R. Field and the two anonymous reviewers for their useful comments and remarks. This study was funded by The European Commission (ECOCHANGE project, contract nr. FP6 2006 GOCE 036866) and NSF grant no. 31003A-125145 (BIOASSEMBLE project). GL is supported by NSF grant CRS113-125240. LP was supported by The Danish Council for Independent Research grant no. 12-126430. The computations were performed at the Vital-IT Center for high-performance computing[1] of the Swiss Institute of Bioinformatics.

References

Amiet, F. (1996) Hymenoptera Apidae, 1. Teil. Allgemeiner Teil, Gattungsschlüssel, die Gattungen Apis, Bombus und Psithyrus. Insecta Helvetica (Fauna) 12, 98pp.

Antonovics, J. & Edwards, M. (2011) Spatio-temporal dynamics of bumblebee nest parasites (Bombus subgenus Psythirus ssp.) and their hosts (Bombus spp.). Journal of Animal Ecology, 80, 999–1011.

Brinck, P. (1974). Strategy and dynamics of high altitude faunas. Arctic and Alpine Research, 6, 107–116.

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.

Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. The American Naturalist, 137, 27–49.

Goulson, D. (2010) Bumblebees: behaviour, ecology, and conservation. Oxford University Press.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. & Knight, M.E. (2005) Causes of rarity in bumblebees. Biological Conservation, 122, 1–8.

Goulson, D., Lye, G.C. & Darvill, B. (2008) Diet breadth, coexistence and rarity in bumblebees. Biodiversity and Conservation, 17, 3269–3288.

Gutiérrez, D. & Menéndez, R. (1998) Phenology of butterflies along an altitudinal gradient in northern Spain. Journal of Zoology, 244, 249–264.

Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S., Mouillot, D. & Poulin, R. (2008) Latitudinal gradients in niche breadth: empirical evidence from haematophagous ectoparasites. Journal of Biogeography, 35, 592–601.

Litsios, G. & Salamin, N. (2012) Effects of phylogenetic signal on ancestral state reconstruction. Systematic Biology, 61, 533–8.

MacArthur, R.H. (1955) Fluctuations of animal populations and a measure of community stability. Ecology, 36, 533–536.

MacArthur, R.H. (1972) Geographical ecology. New York: Harper & Row.

Martin, S.J., Carruthers, J.M., Williams, P.H. & Drijfhout, F. P. (2010) Host specific social parasites (Psithyrus) indicate chemical recognition system in bumblebees. Journal of Chemical Ecology, 36, 855–63.

Orme, C.D.L., Freckleton, R.P., Thomas, G.H., Pedzoldt, T. & Fritz, S. (2011) Caper: comparative analyses of phylogenetics and evolution in R.

Parker, G. & Stuart, R. (1976) Animal behavior as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. The American Naturalist, 110, 1055–1076.

Pellissier, L., Litsios, G., Fiedler, K., Pottier, J., Dubuis, A., Pradervand, J.-N., Salamin, N. & Guisan, A. (2012a) Loss of interactions with ants under cold climate in a regional myrmecophilous butterfly fauna. Journal of Biogeography, 39, 1782–1790.

Pellissier, L., Pradervand, J.-N., Williams, P.H., Litsios, G., Cherix, D. & Guisan, A. (2012b) Phylogenetic relatedness and proboscis length contribute to structuring bumblebee communities in the extremes of abiotic and biotic gradients. Global Ecology and Biogeography, 22, 577–585.

Pradervand, J.-N., Pellissier, L., Rossier, L., Dubuis, A., Guisan, A. & Cherix, D. (2011) Les Alpes vaudoises, un havre de diversité pour les bourdons (Bombus Latreille, Apidae). Mitteilungen der Schweizerischen entomologischen Gesellschaft – Bulletin de la Société Entomologique Suisse, 84, 46–66.

Rapoport, E.H. (1975) Areografia: estrategias geograficas de las especies. Mexico City: Fondo de Cultura Economica.

---

[1] http://www.vital-it.ch

Rasmont, P. (1988) Monographie écologique et zoogéographique des Bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae). PhD thesis, Faculté des Sciences agronomiques de l'Etat, Gembloux, 309+LXIIpp.

Roulston, T.H. & Goodell, K. (2011) The role of resources and risks in regulating wild bee populations. Annual Review of Entomology, 56, 293–312.

Sanders, N.J. (2002) Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. Ecography, 25, 25–32.

Stevens, G.C. (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. The American Naturalist, 140, 893–911.

Stireman, J.O., Dyer, L.A., Janzen, D.H. et al. (2005) Climatic unpredictability and parasitism of caterpillars: implications of global warming. Proceedings of the National Academy of Sciences of the United States of America, 102, 17384–17387.

Vázquez, D.P. & Stevens, R.D. (2004) The latitudinal gradient in niche breadth: concepts and evidence. The American Naturalist, 164, 1–19.

Wcislo, W.T. (1987) Parasitism rates in relation to nest site in bees and wasps (Hymenoptera: Apoidea). Journal of Insect Behavior, 9, 643–656.

Williams, P. (2008) Do the parasitic Psithyrus resemble their host bumblebees in colour pattern? Apidologie, 39, 637–649.

Yom-Tov, Y. & Geffen, E. (2005) Host specialization and latitude among cuckoos. Journal of Avian Biology, 36, 465–470.

Zimmermann, N. & Kienast, F. (1999) Predictive mapping of alpine grasslands in Switzerland: species versus community approach. Journal of Vegetation Science, 10, 469–482.

Edited by Jan Beck