

Research



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Community ecology

Wind drives temporal variation in pollinator visitation in a fragmented tropical forest

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Wind is a critical factor in the ecology of pollinating insects such as bees. However, the role of wind in determining patterns of bee abundance and floral visitation rates across space and time is not well understood. Orchid bees are an important and diverse group of neotropical pollinators that harvest pollen, nectar and resin from plants. In addition, male orchid bees collect volatile scents that they store in special chambers in their hind legs, and for which the wind-based dispersal of odours may play a particularly crucial role. Here, we take advantage of this specialized scent foraging behaviour to study the effects of wind on orchid bee visitation at scent sources in a fragmented tropical forest ecosystem. Consistent with previous work, forest cover increased orchid bee visitation. In addition, we find that temporal changes in wind speed and turbulence increase visitation to scent stations within sites. These results suggest that the increased dispersal of attractive scents provided by wind and turbulence outweighs any biomechanical or energetic costs that might deter bees from foraging in these conditions. Overall, our results highlight the significance of wind in the ecology of these important pollinators in neotropical forests.

1. Introduction

Animal pollinators such as bees provide critical ecosystem services that support biodiversity [1] and global crop yields [2]. The composition and abundance of pollinator communities can vary substantially in both space [3] and time [4], likely as a result of both stochastic fluctuations and small-scale variation in the biotic and abiotic environment [5].

Wind strongly affects flying insects and may be an important factor in spatio-temporal heterogeneity of pollinator visitation. Wind affects macroecological patterns of insect dispersal and migration [6,7]. Mean wind flow [8] and fluctuations (i.e. turbulence) pose biomechanical challenges [9–13] that push manoeuvrability limits in flying insects [14] and can impose energetic costs on flight [15]. The mechanical and physiological challenges posed by wind may have important effects on insects' interactions with plants, including herbivory [16,17], and pollinator visitation and landing [18]. Wind also indirectly impacts flying insects by inducing plant movements [19], which can impose additional manoeuvrability challenges [14].

In addition to biophysical challenges, wind disperses chemical cues and signals critical for interactions between insects (e.g. attracting mates [20], or locating prey [21,22]), as well as between insects and plants (e.g. pollinator attraction [23–25] and herbivory [26]). Turbulence (i.e. fluctuations in wind

on top of mean flow speed and direction) is a critical factor in olfactory navigation, as it disperses odours into complex plumes [27,28].

While wind is known to have many effects on pollinator behaviour and ecology, our understanding of its influence on bee abundance and plant visitation rates is limited. While extreme wind speeds restrict bee flight and foraging (reviewed in [29]), recent studies have found that wind can have either positive [30] or negligible [10,31] effects on bee abundance and activity. Some of the variable effects of wind could be explained by differences in sensory ecology, particularly the importance of olfactory cues for locating floral resources.

Orchid bees (Apidae: Euglossini) are a key group of pollinators for which wind-borne odours likely play a uniquely critical role. The approximately 200 species (across four genera) of orchid bees are important neotropical pollinators of orchids and several other plant families [32], in addition to pollinating important crop plants such as tomato [33,34]. In this group, foraging behaviour intersects with mating strategies, as male orchid bees gather species-specific combinations of volatile compounds from a wide variety of flower species [35]. These fragrance 'bouquets' are thought to play a key role in attracting mates [36]. Orchid bees are primarily forest associated, and they collect fragrances from flowers and other sources that are often sparsely distributed within tropical rainforests. Accordingly, male orchid bees show strong patterns of long-distance movement and dispersal across the landscape [37–40] and are thought to locate floral scent resources in dense vegetation using olfactory cues.

Despite its likely importance in dispersing scents, the role of wind in orchid bee ecology is not well understood, although previous observers have noted temporary increases in orchid bee arrivals at baits after wind gusts [41]. Recent work has also shown that male orchid bees performing mating displays strongly prefer to orient on the downwind side of trees, presumably to maximize the dispersal of odour plumes [42]. However, to our knowledge, quantitative studies of the impacts of wind (or turbulence) on spatial or temporal variation in orchid bee abundance and visitation rates at scent sources have not been made.

Local wind patterns can be strongly affected by forest fragmentation [43], which is increasingly characteristic of the Neotropical range of orchid bees. Previous work has shown that forest fragmentation significantly alters orchid bee communities (compared to continuous forest [44]), and some studies have found that fragment traits (such as size and shape) significantly affect orchid bee abundance and community composition [45–47] (although other studies have not found evidence for such a relationship [48,49]). In addition to variation across fragments, abundance and composition of orchid bee communities can vary locally within fragments, for example as a result of microhabitat variation [47,50,51] and edge effects [52,53]. Recent work has also shown that local landscape structure (e.g. forested area within 1000 m) can have significant effects on bee community structure and abundance [54].

Here, we explore the effects of local landscape structure, wind speed and turbulence on male orchid bee visitation rates to scent sources within and adjacent to a large tropical forest fragment. In addition to a positive association between visitation and local forest cover, we predict that wind speed positively correlates with orchid bee visitation, because higher wind speeds will further disperse scents and attract bees from a wider area. Conversely, we hypothesize that

turbulence is negatively correlated with visitation, because stronger turbulence will result in higher costs of flight and make odour plumes more challenging for bees to track.

2. Material and methods

(a) Sampling sites and orchid bee collection

We collected male orchid bees from nine different sites within or adjacent to a large forest fragment at the Las Cruces Biological Station (8.79°, –82.96°) in Coto Brus, Puntarenas Province, Costa Rica (figure 1, electronic supplementary material, table S1). The forested areas in this region are characterized by premontane forest, with a high abundance and diversity of euglossine bees [45].

Male orchid bees were collected from each site multiple (5–9) times between 1 October and 16 November 2014 (electronic supplementary material, table S2). All collections occurred between 08.30 and 11.30, roughly corresponding to peak daily abundance. Bees were sampled by saturating tissue paper with one of two compounds (cineole or methyl salicylate) and suspending this scent bait approximately 1.5 m above the ground in a permeable metal tea infuser. Male orchid bees arriving at the scent bait were collected by hand netting for 20 min. Bees were identified (electronic supplementary material, table S1) independently by two authors (J.B. and J.D.C.) using an established taxonomic key [55]. Identifications of example specimens for each species were reviewed and corrected by Dr Santiago Ramírez (UC Davis).

(b) Wind measurement

Simultaneous with bee collections, we characterized the local wind environment using a three-dimensional sonic anemometer operating at 10 Hz placed 1 m above the ground and greater than 4 m away from the scent bait. For each 20 min wind sample, we calculated the mean wind speed and turbulence. We estimated the strength of turbulence by measuring the mass-specific turbulent kinetic energy of wind (*TKE*), as $0.5 * (\sigma^2(u - \bar{u}) + \sigma^2(v - \bar{v}) + \sigma^2(w - \bar{w}))$ following [56], where *u*, *v* and *w* represent wind speeds in the East–West, North–South and vertical direction, respectively, \bar{u} , \bar{v} and \bar{w} represent mean values along those respective axes, and σ^2 represents variance. Overall mean wind speed was calculated as $\sqrt{\bar{u}^2 + \bar{v}^2 + \bar{w}^2}$. As turbulent kinetic energy correlated strongly with wind speed, we estimated the relative turbulent kinetic energy (hereafter 'relative TKE') as the residuals of a linear model of *TKE* on mean wind speed ($\log_{10}(TKE) \sim \log_{10}(\text{mean wind speed})$).

(c) Estimation of landscape forest cover

To estimate the local forest cover at each site, we used a manually digitized GIS layer of small-scale (approx. 2 m resolution) forest elements in the region [57,58]. We calculated the extent of forest cover (% area forested) within a 200 m buffer radius around each site (figure 1). Using alternative buffer distances of 100–500 m had no qualitative effect on results.

(d) Data analysis and statistics

We built a generalized linear mixed effects model (Poisson family with a log-link) to assess factors driving orchid bee visitation (i.e. the total number of male orchid bees visiting a bait during a collection) using the 'lme4' package [59] in R [60]. Forest cover within 200 m, wind speed and turbulence (relative TKE) were included as fixed effects in this model, while collection site and date were included as random effects. *p*-Values were calculated using the 'lmerTest' package [61]. Interaction effects between forest cover and wind speed, and forest cover and turbulence, were not significant, and were removed from the final model. Excluding collections where methyl salicylate was used as a bait



Figure 1. Study area and methods. (a) Map of collection sites ($N = 9$) at Las Cruces Biological Station, Puntarenas Province, Costa Rica. Solid markers show collection site (with shade indicating average percentage of local forest cover), and dotted lines show buffer zones used for measuring forest cover (radius = 200 m). (b) Male orchid bees visiting a scent bait. (c) Three-dimensional sonic anemometer deployed in the field. Photos: Julia Brokaw.

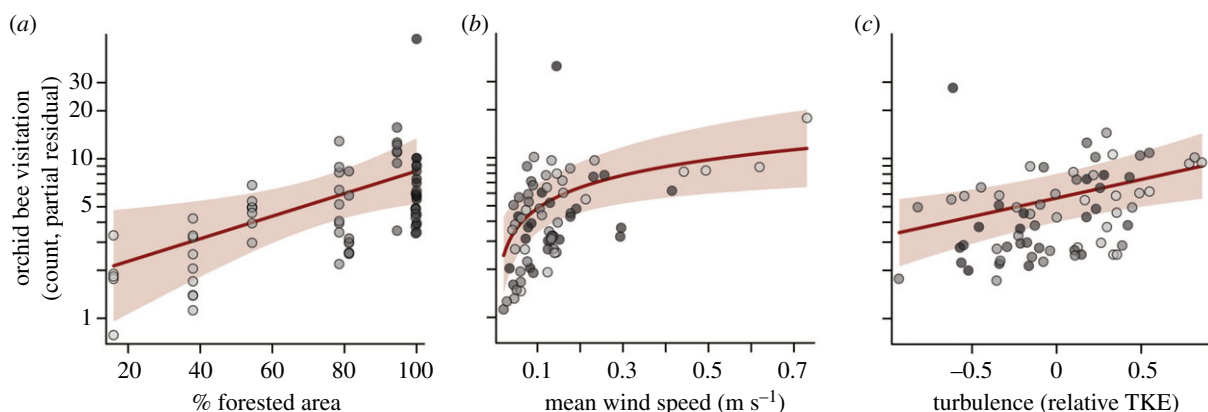


Figure 2. Forest cover and wind drive orchid bee visitation. Marginal effect plots for (a) forest cover (% within 200 m), (b) the effects of wind speed and (c) turbulence on orchid bee visitation. Solid markers show partial residuals for individual collections. Marker shade in all figures indicates amount of forested area (equivalent to site colours in figure 1).

(which represented a minority of collections) had no qualitative effects on results, so collections made with methyl salicylate and cineole were pooled. We built a separate generalized linear model to directly test effects of wind among (versus within) sites (see electronic supplementary material, figure S1 for details).

Data and custom scripts are available on Zenodo (<https://doi.org/10.5281/zenodo.3743898>).

3. Results

We collected a total of 409 male orchid bees, from 23 different species (electronic supplementary material, table S3). Orchid bee visitation varied significantly among sites (Kruskal–Wallis test, $\chi^2 = 26.2$, d.f. = 8, $p = 9.7 \times 10^{-4}$) and was positively correlated with the percentage of forested area within 200 m of collection sites (figure 2a, generalized linear mixed model,

d.f. = 64, $z = 2.56$, $p = 0.01$). In addition, we found that wind speed had a significant, positive effect on orchid bee visitation over time within sites (figure 2b, generalized linear mixed model, d.f. = 64, $z = 3.45$, $p = 0.0005$). Turbulence also had a significant positive effect on orchid bee visitation (figure 2c, generalized linear mixed model, d.f. = 64, $z = 2.87$, $p = 0.004$).

The same positive effects of wind speed and turbulence on visitation were not found between sites. Both wind speed and turbulence also varied significantly between sites (Kruskal–Wallis test; wind speed, $\chi^2 = 31.3$, d.f. = 8, $p = 0.0001$; relative TKE, $\chi^2 = 24.1$, d.f. = 8, $p = 0.02$). However, sites with higher average wind speeds did not have higher median visitation (electronic supplementary material, figure S1A). Likewise, sites with higher mean turbulence did not have higher median visitation (electronic supplementary material, figure S1B).

4. Discussion

Our results suggest that both landscape and wind play important roles in driving male orchid bee visitation rates. In particular, our findings support previous observations that orchid bee communities can vary significantly across small spatial scales (i.e. less than 1 km) [47,50,52] and suggest that forest cover in particular has important effects on local variations in orchid bee abundance. This supports previous work showing that local forested area (within 1000 m) can significantly alter the composition and abundance of bee communities in general [54], and orchid bee communities in particular [49]. Our findings show that these effects occur on even shorter spatial scales (i.e. 200 m) and can drive spatial variation within forested fragments.

We also found a significant, positive effect of wind speed on visitation rates over time within sites (figure 2b), despite relatively low wind speeds (median wind speed of 0.122 m s^{-1} , versus a global terrestrial average of approximately $3.1\text{--}3.4 \text{ m s}^{-1}$ [62]). The simplest explanation of this pattern is that increased wind speeds disperse attractive scents over greater distances, attracting male orchid bees from a wider area.

The positive association between wind speed and visitation within sites does not hold true between sites, as windier sites did not have higher visitation (electronic supplementary material, figure S1). A possible explanation for this pattern is that spatial variation (i.e. between sites) in orchid bee male abundance is primarily driven by local landscape context, while temporal variation (i.e. within sites) in visitation is more strongly affected by wind. For example, increased forest cover may increase the number of individuals located near a site at any given time, while higher wind speeds may increase the likelihood of those individuals visiting a scent source.

We found no evidence that turbulence decreases orchid bee visitation; instead, higher relative turbulence was positively associated with visitation (figure 2c). While turbulence is often considered a challenge for olfactory navigation, we speculate that a possible explanation for this result is that turbulence also plays a role in dispersing attractive odours via turbulent diffusion, an effect that could be especially important when mean wind speeds are low.

Overall, our results underscore the importance of wind for pollinator ecology, particularly in species that rely strongly on olfactory cues. Previous work has noted that orchid bee

abundance can vary significantly across time within sites [45]. Our results are consistent with these observations and suggest that temporal variation within sites is driven, in part, by variation in wind speed and turbulence, consistent with previous anecdotal observations [48]. Future studies investigating a wider range of environmental conditions and a diversity of pollinator species will be critical for understanding the generality of the findings here (e.g. whether the positive effects of wind are restricted to species that rely primarily on olfactory cues).

These results may also have important implications for the timing of volatile release in Euglossine bee-attracting plants. The release of pollinator-attracting fragrances from many flowers shows strong rhythmicity, likely synchronized with the activity of pollinating animals [63]. Our findings suggest that timing and efficacy of scent release by flowering plants could also be shaped by wind conditions.

More broadly, our results underscore the potentially important but understudied role of wind in pollinator behaviour and ecology. In addition, anthropogenic environmental change is altering wind conditions at both the local (e.g. forest fragmentation [43,64]) and global (e.g. planetary shifts in wind and weather patterns [62,65]) scales. However, the effects of these changes on pollinators and the ecosystem services they provide are not well understood and represent an important direction for future study.

Data accessibility. Raw data and custom scripts are available on Zenodo <https://doi.org/10.5281/zenodo.3743898> [66].

Authors' contributions. J.D.C., N.E.P. and S.A.C. conceived and designed the study. J.D.C., S.G. and J.B. collected data on orchid bees and wind. C.D.M. generated landscape data. J.D.C. analysed data and performed statistical analyses. All authors contributed to writing and editing the manuscript. All authors agree to be held accountable for the content herein and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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References

- Ollerton J, Winfree R, Tarrant S. 2011 How many flowering plants are pollinated by animals? *Oikos* **120**, 321–326. (doi:10.1111/j.1600-0706.2010.18644.x)
- Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Scharntke T. 2007 Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* **274**, 303–313. (doi:10.1098/rspb.2006.3721)
- Edwards J, Griffin AJ, Knodler MR. 2018 Simultaneous recordings of insect visitors to flowers show spatial and temporal heterogeneity. *Ann. Entomol. Soc. Am.* **117**, 93–98. (doi:10.1093/aesa/say044).
- Olesen JM, Bascompte J, Elberling H, Jordano P. 2008 Temporal dynamics in a pollination network. *Ecology* **89**, 1573–1582. (doi:10.1890/07-0451.1)
- Herrera CM. 1995 Microclimate and individual variation in pollinators: flowering plants are more than their flowers. *Ecology* **76**, 1516–1524. (doi:10.2307/1938153)
- Hu G, Lim KS, Reynolds DR, Reynolds AM, Chapman JW. 2016 Wind-related orientation patterns in diurnal, crepuscular and nocturnal high-altitude insect migrants. *Front. Behav. Neurosci.* **10**, 1221–1228. (doi:10.3389/fnbeh.2016.00032)
- Hu G, Lim KS, Horvitz N, Clark SJ, Reynolds DR. 2016 Mass seasonal bioflows of high-flying insect migrants. *Science* **354**, 1584–1587. (doi:10.1126/science.aah4379)
- Riley JR, Reynolds DR, Smith AD, Edwards AS, Osborne JL, Williams IH, McCartney HA. 1999 Compensation for wind drift by bumble-bees. *Nature* **400**, 126. (doi:10.1038/22029)
- Ravi S, Crall JD, Fisher A, Combes SA. 2013 Rolling with the flow: bumblebees flying in unsteady wakes. *J. Exp. Biol.* **216**, 4299–4309. (doi:10.1242/jeb.090845)
- Crall JD, Chang JJ, Oppenheimer RL, Combes SA. 2017 Foraging in an unsteady world: bumblebee flight performance in field-realistic turbulence. *Interface Focus* **7**, 20160086. (doi:10.1098/rsfs.2016.0086)
- Ortega-Jimenez VM, Greeter JSM, Mittal R, Hedrick TL. 2013 Hawkmoth flight stability in turbulent vortex streets. *J. Exp. Biol.* **216**, 4567–4579. (doi:10.1242/jeb.089672)
- Ortega-Jimenez VM, Mittal R, Hedrick TL. 2014 Hawkmoth flight performance in tornado-like

- whirlwind vortices. *Bioinspir. Biomim.* **9**, 1–12. (doi:10.1088/1748-3182/9/2/025003)
13. Matthews M, Sponberg S. 2018 Hawkmoth flight in the unsteady wakes of flowers. *J. Exp. Biol.* **221**, 1–13. (doi:10.1242/jeb.179259)
 14. Mountcastle AM, Ravi S, Combes SA. 2015 Nectar vs. pollen loading affects the tradeoff between flight stability and maneuverability in bumblebees. *Proc. Natl Acad. Sci. USA* **112**, 10 527–10 532. (doi:10.1073/pnas.1506126112)
 15. Combes SA, Dudley R. 2009 Turbulence-driven instabilities limit insect flight performance. *Proc. Natl Acad. Sci. USA* **106**, 9105–9108. (doi:10.1073/pnas.0902186106)
 16. Cherry MJ, Barton BT. 2017 Effects of wind on predator–prey interactions. *Food Webs* **13**, 92–97. (doi:10.1016/j.fooweb.2017.02.005)
 17. Barton BT. 2014 Reduced wind strengthens top-down control of an insect herbivore. *Ecology* **95**, 2375–2381. (doi:10.1890/13-2171.1)
 18. Chang JJ, Crall JD, Combes SA. 2016 Wind alters landing dynamics in bumblebees. *J. Exp. Biol.* **219**, 2819–2822. (doi:10.1242/jeb.137976)
 19. de Langre E. 2008 Effects of wind on plants. *Annu. Rev. Fluid Mech.* **40**, 141–168. (doi:10.1146/annurev.fluid.40.111406.102135)
 20. Kennedy JS, Ludlow AR, Sanders CJ. 1981 Guidance of flying male moths by wind-borne sex pheromone. *Physiol. Entomol.* **6**, 395–412. (doi:10.1111/j.1365-3032.1981.tb00655.x)
 21. Vet LE, Groenewold AW. 1990 Semiochemicals and learning in parasitoids. *J. Chem. Ecol.* **16**, 3119–3135. (doi:10.1007/BF00979615)
 22. Tumlinson JH, Lewis WJ, Vet LEM. 1993 How parasitic wasps find their hosts. *Sci. Am.* **266**, 100–106. (doi:10.1038/scientificamerican0393-100)
 23. Fuentes JD, Chamecki M, Roulston T, Chen B, Pratt KR. 2016 Air pollutants degrade floral scents and increase insect foraging times. *Atmos. Environ.* **141**, 361–374. (doi:10.1016/j.atmosenv.2016.07.002)
 24. Stensmyr MC, Urru I, Collu I, Celander M, Hansson BS, Angioy A-M. 2002 Pollination: rotting smell of dead-horse arum florets. *Nature* **420**, 625–626. (doi:10.1038/420625a)
 25. Wang TN, Clifford MR, Martínez-Gómez J, Johnson JC, Riffell JA, Di Stilio VS. 2018 Scent matters: differential contribution of scent to insect response in flowers with insect vs. wind pollination traits. *Ann. Bot.* **123**, 289–301. (doi:10.1093/aob/mcy131)
 26. Pare P, Tumlinson J. 1999 Plant volatiles as a defense against insect herbivores. *Plant Physiol.* **121**, 325–332. (doi:10.1104/pp.121.2.325)
 27. Murlis J, Jones C. 1981 Fine-scale structure of odour plumes in relation to insect orientation to distant pheromone and other attractant sources. *Physiol. Entomol.* **6**, 71–86. (doi:10.1111/j.1365-3032.1981.tb00262.x)
 28. Murlis J, Willis MA, Cardé RT. 2000 Spatial and temporal structures of pheromone plumes in fields and forests. *Physiol. Entomol.* **25**, 211–222. (doi:10.1046/j.1365-3032.2000.00176.x)
 29. Kevan PG, Baker HG. 1983 Insects as flower visitors and pollinators. *Annu. Rev. Entomol.* **28**, 407–453. (doi:10.1146/annurev.en.28.010183.002203)
 30. Arce AN, David TI, Randall EL, Rodrigues AR, Colgan TJ, Wurm Y, Gill RJ. 2016 Impact of controlled neonicotinoid exposure on bumblebees in a realistic field setting. *J. Appl. Ecol.* **54**, 1199–1208. (doi:10.1111/1365-2664.12792)
 31. Kremen C, Williams NM, Bugg RL, Fay JP, Thorp RW. 2004 The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Letters* **7**, 1109–1119. (doi:10.1111/j.1461-0248.2004.00662.x)
 32. Dressler RL. 1982 Biology of the orchid bees (Euglossini). *Annu. Rev. Ecol. Syst.* **13**, 373–394. (doi:10.1146/annurev.es.13.110182.002105)
 33. Silva-Neto CM, Bergamini LL, Elias M, Moreira G, Morais JM, Bergamini B, Franceschinelli EV. 2017 High species richness of native pollinators in Brazilian tomato crops. *Braz. J. Biol.* **77**, 506–513. (doi:10.1590/1519-6984.17515)
 34. Bergamini B, Lima FG, Gonçalves BB, Bergamini LL, Bergamini BAR, da Silva Elias MA, Franceschinelli EV. 2013 Native bees pollinate tomato flowers and increase fruit production. *J. Pollinat. Ecol.* **11**, 41–45. (doi:10.26786/1920-7603(2013)4)
 35. Zimmermann Y, Ramírez SR, Eltz T. 2009 Chemical niche differentiation among sympatric species of orchid bees. *Ecology* **90**, 2994–3008. (doi:10.1890/08-1858.1)
 36. Eltz T, Roubik DW, Whitten MW. 2003 Fragrances, male display and mating behaviour of *Euglossa hemichlora*: a flight cage experiment. *Physiol. Entomol.* **28**, 251–260. (doi:10.1111/j.1365-3032.2003.00340.x)
 37. Suni SS. 2016 Dispersal of the orchid bee *Euglossa imperialis* over degraded habitat and intact forest. *Conserv. Genet.* **18**, 621–630. (doi:10.1007/s10592-016-0902-x)
 38. Suni SS, Bronstein JL, Brosi BJ. 2014 Spatio-temporal genetic structure of a tropical bee species suggests high dispersal over a fragmented landscape. *Biotropica* **46**, 202–209. (doi:10.1111/btp.12084)
 39. Pokorny T, Loose D, Dyker G, Quezada-Euán JGG, Eltz T. 2014 Dispersal ability of male orchid bees and direct evidence for long-range flights. *Apidologie* **46**, 224–237. (doi:10.1007/s13592-014-0317-y)
 40. Wikelski M, Moxley J, Eaton-Mordas A, López-Uribe MM, Holland R, Moskowitz D, Roubik DW, Kays R. 2010 Large-range movements of neotropical orchid bees observed via radio telemetry. *PLoS ONE* **5**, e10738-6. (doi:10.1371/journal.pone.0010738)
 41. Tonhasca Jr A, Blackmer JL, Albuquerque GS. 2002 Within-habitat heterogeneity of euglossine bee populations: a re-evaluation of the evidence. *J. Trop. Ecol.* **18**, 929–933. (doi:10.1017/S0266467402002602)
 42. Pokorny T, Vogler I, Losch R, Schlütting P, Juarez P, Bissantz N, Ramírez SR, Eltz T. 2017 Blown by the wind: the ecology of male courtship display behavior in orchid bees. *Ecology* **98**, 1140–1152. (doi:10.1002/ecy.1755)
 43. Damschen El *et al.* 2014 How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. *Proc. Natl. Acad. Sci. USA* **111**, 3484–3489. (doi:10.1073/pnas.1308968111)
 44. Botsch JC. 2017 Impacts of forest fragmentation on orchid bee (Hymenoptera: Apidae: Euglossini) communities in the Chocó biodiversity hotspot of northwest Ecuador. *J. Insect Conser.* **21**, 633–643. (doi:10.1007/s10841-017-0006-z)
 45. Brosi BJ. 2009 The effects of forest fragmentation on euglossine bee communities (Hymenoptera: Apidae: Euglossini). *Biol. Conser.* **142**, 414–423. (doi:10.1016/j.biocon.2008.11.003)
 46. Storck-Tonon D, Morato EF, de Melo AWF, de Oliveira ML. 2013 Orchid bees of forest fragments in Southwestern Amazonia. *Biota Neotropica* **13**, 133–141. (doi:10.1590/S1676-0603201300100015)
 47. Becker P, Moure JS, Peralta FJ. 1991 More about euglossine bees in Amazonian forest fragments. *Biotropica* **23**, 586–591. (doi:10.2307/2388396)
 48. Tonhasca Jr A, Blackmer JL, Albuquerque GS. 2002 Abundance and diversity of Euglossine bees in the fragmented landscape of the Brazilian Atlantic forest. *Physiol. Entomol.* **34**, 416–422. (doi:10.1111/j.1744-7429.2002.tb00555.x)
 49. Cândido MEMB. 2018 Effects of fragments and landscape characteristics on the orchid bee richness (Apidae: Euglossini) in an urban matrix, southwestern Amazonia. *J. Insect Conser.* **22**, 475–486. (doi:10.1007/s10841-018-0075-7)
 50. Sobreiro AI, Peres LLDS, Boff S, Henrique JA, Alves Junior VV. 2019 Continuous micro-environments associated orchid bees benefit from an Atlantic Forest Remnant, Paraná State, Brazil. *Sociobiology* **66**, 293–305. (doi:10.13102/sociobiology.v66i2.3443)
 51. Armbruster WS. 1993 Within-habitat heterogeneity in baiting samples of male euglossine bees: possible causes and implications. *Biotropica* **25**, 122–128. (doi:10.2307/2388986)
 52. Nemésio A, Silveira FA. 2006 Edge effects on the orchid-bee fauna (Hymenoptera: Apidae) at a large remnant of Atlantic Rain Forest in southeastern Brazil. *Neotrop. Entomol.* **35**, 313–323. (doi:10.1590/S1519-566X2006000300004)
 53. Mullally HL, Buckley DS, Fordyce JA, Collins B, Kwit C. 2019 Bee communities across gap, edge, and closed-canopy microsites in forest stands with group selection openings. *Forest Sci.* **65**, 751–757. (doi:10.1093/forsci/afx035)
 54. Gutiérrez-Chacón C, Dormann CF, Klein A-M. 2018 Forest-edge associated bees benefit from the proportion of tropical forest regardless of its edge length. *Biol. Conser.* **220**, 149–160. (doi:10.1016/j.biocon.2018.02.009)
 55. Roubik DW, Hanson PE. 2004 *Orchid bees of tropical america: biology and field guide*. Heredia, Costa Rica: Instituto Nacional de Biodiversidad.
 56. Stull RB. 2012 *An introduction to boundary layer meteorology*. Dordrecht, The Netherlands: Kluwer Academic Publishers.
 57. Mendenhall CD, Sekercioglu CH, Brenes FO, Ehrlich PR, Daily GC. 2011 Predictive model for sustaining biodiversity in tropical countryside. *Proc. Natl Acad.*

- Sci. USA* **108**, 16 313–16 316. (doi:10.1073/pnas.1111687108)
58. Mendenhall CD, Wrona AM. 2018 Improving tree cover estimates for fine-scale landscape ecology. *Landscape Ecology* **33**, 1691–1696. (doi:10.1007/s10980-018-0704-2)
59. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
60. R Core Team. 2013 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
61. Kuznetsova A, Brockhoff PB, Christensen HB. 2014 lmerTest: tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package), v. 2.0–25. See <https://github.com/runehaubo/lmerTestR>.
62. Zeng Z *et al.* 2019 A reversal in global terrestrial stilling and its implications for wind energy production. *Nat. Clim. Change* **9**, 979–985. (doi:10.1038/s41558-019-0622-6)
63. Matile P, Altenburger R. 1988 Rhythms of fragrance emission in flowers. *Planta* **174**, 242–247. (doi:10.1007/BF00394777)
64. Magnago LFS, Rocha MF, Meyer L, Martins SV, Meira-Neto JAA. 2015 Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. *Biodivers. Conser.* **24**, 1–15. (doi:10.1007/s10531-014-0770-y)
65. Vautard R, Cattiaux J, Yiou P, Thépaut J-N, Ciais P. 2010 Northern Hemisphere atmospheric stilling partly attributed to an increase in surface roughness. *Nat. Geosci.* **3**, 1–6. (doi:10.1038/ngeo979)
66. Crall JD, Brokaw J, Gagliardi SF, Mendenhall CD, Pierce NE, Combes SA. 2020 Wind drives temporal variation in pollinator visitation in a fragmented tropical forest. Zenodo. (<https://doi.org/10.5281/zenodo.3743898>)