

CONSERVATION

The trouble with bumblebees

A survey of bumblebees in North America provides unequivocal evidence that four previously common and abundant species have undergone recent and widespread population collapse. Various explanations remain possible.

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“**T**o make a prairie it takes a clover and one bee, One clover, and a bee. And revery. The revery alone will do, If bees are few.”¹ Bumblebees, the main pollinators of red clover and much else besides, comprise a genus of some 250 species that are central both to natural ecosystem function and to a multimillion-pound commercial pollination industry involving the production and global traffic of bumblebee colonies². Unfortunately, bumblebees may indeed be becoming ‘few’. Recently there have been disturbing reports of rapid declines in North American species, with speculation that the declines are being driven by introduced parasites³.

Writing in *Proceedings of the National Academy of Sciences*⁴, Cameron *et al.* now provide evidence of geographically widespread and temporally rapid reductions in the distribution and abundance of four bumblebee species across the contiguous United States. The species, which constitute about 10% of the regional bumblebee species, had both lower genetic variability and significantly higher prevalence (the percentage of the population infected) of the microsporidian parasite *Nosema bombi* — a type of fungus that has been implicated as a potential cause of bumblebee decline.

Bumblebee decline is not a new story. Since the problem was first recognized in Britain in the 1950s, numerous studies have documented long-term deteriorations in species ranges, with habitat loss being the generally accepted cause². What makes reports from North America both worrying and intriguing is the apparent speed of the deterioration.

To test the rapidity and extent of the declines, Cameron *et al.*⁴ generated a database of historical collections from across the United States and used it, together with niche modelling software, to estimate species distribution and patterns of relative abundance since 1900 for eight target species, half of which had previously been suggested to be in decline. Current distribution and relative abundance were determined by sampling at 382 sites across 40 states between 2007 and 2009. The range of four species — *Bombus affinis*, *B. occidentalis*, *B. pensylvanicus* (Fig. 1) and *B. terricola* — had decreased by 23–87%, with the other four



Figure 1 | *Bombus pensylvanicus* — in decline.

species being, as expected, present in most of their historical range. The affected species also exhibited rapid declines — over the past 20–30 years — in relative abundance.

As the authors acknowledge, local species extinction is notoriously hard to prove, and the over-representation of rare species in historical collections makes determining relative abundance problematic. Such difficulties mean that the exact extent and rate of each decline reported in this study is open to question. But the basic result — that previously common and abundant bumblebee species have undergone recent, widespread population collapse — seems undeniable. So, what is driving these declines?

Emergent diseases are increasingly being recognized as threats to both humans and native species⁵. Pathogen transmission from commercially bred colonies to natural populations has already been seen in two other parasites of bumblebees⁶. Rapid falls in numbers of North American bumblebees, redolent of an epidemic, were contemporaneous with the collapse in commercial breeding of *B. occidentalis* in North America, which was blamed on *N. bombi*. These observations led to the hypothesis that *N. bombi*, introduced from Europe by means of commercial pollinators to native bumblebees, was driving declines³. Cameron and colleagues show that *N. bombi* indeed has significantly higher prevalence in the rapidly failing species. Furthermore, DNA sequencing demonstrated that these North

American parasites were genetically identical to European isolates.

Is this the smoking gun behind North American bumblebee declines? To answer this question, we need to know what high parasite prevalence means.

There are two obvious interpretations. First, high parasite prevalence may represent the moving edge of a wave of infections, indicating that these bumblebee populations are on the verge of extinction. Similar patterns in the fungus responsible for global amphibian declines, albeit in the intensity (number of parasite cells per individual) rather than prevalence of infection, precede local extinction of amphibians⁷. Second, high prevalence may simply indicate that the declining species naturally support high populations of the parasite.

Is there any evidence to distinguish between these interpretations? Alaskan populations of *B. occidentalis*, which remain abundant, also have a high prevalence of infection by *N. bombi* (J. P. Strange, personal communication), but this could support either explanation. Intriguingly, a parasitic mite of bumblebees has higher prevalence in species of the subgenus *Bombus* in Canada⁸, the same subgenus to which three of the four declining species belong. This supports the idea that the species are natural reservoirs for the microsporidian. By contrast, the genetic identity between North American parasites and European isolates is evidence for the emergent-disease interpretation (although large-scale genetic studies are needed to confirm this).

A final ambiguity in understanding the parasite data is that Cameron *et al.*⁴ also found lower genetic diversity in the declining species. Low diversity is predicted to increase susceptibility to parasites, and a recent study demonstrated a correlation between inbreeding and the prevalence of a trypanosome parasite in bumblebees⁹. Untangling the causal direction of correlations between patterns of decline, parasite prevalence and loss of genetic diversity in North American bumblebees will take considerable work.

This study⁴ is the first step towards understanding declines in North American bumblebees, but it also has broader implications. The methodology can be used to track declines in other species for which long-term recording schemes do not exist, a situation that applies to most of the planet's biodiversity. More specifically, global transport of commercial bumblebee colonies sets the stage for pathogen transmission to native species. If *N. bombi* has driven North American declines — and ascertaining this will require further investigation — it and other parasites may have the potential to drive native bumblebee decline across the world.

At a meeting held by the International Union for Conservation of Nature in St Louis, Missouri, in November 2010, commercial producers, non-governmental organizations, federal agencies and scientists discussed measures for conserving native bumblebee species

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while maintaining them as essential commercial pollinators. With due respect to Emily Dickinson¹, 'revery' will not be enough if we want to see prairies, and other important terrestrial ecosystems, thriving in the future. ■

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EARTH SCIENCE

A back-arc in time

The Eastern Lau spreading centre in the Pacific Ocean is the subject of especial interest. The influence of the neighbouring subduction zone is considerable, but evidently has unexpected limits. SEE LETTER P.198

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In plate-tectonic theory, ocean crust and the associated lithosphere are recycled back into Earth's mantle at the destructive plate boundaries called subduction zones. Several subduction zones also have submarine spreading centres that occur on the overriding plate lying behind the arc of surface volcanoes to be found above the site of subduction. These 'back-arc' spreading centres are the most rapidly changing plate-tectonic boundaries on the planet. New ocean crust is constructed by sea-floor spreading at back-arc spreading centres, just as occurs at mid-ocean ridges. But this spreading propels the back-arc spreading centre over the chemically diverse mantle of the subduction zone, and eventually away from the supply of subducted material that feeds the spreading.

On page 198 of this issue¹, Dunn and Martinez describe a study of crustal thickness and structure at the Eastern Lau spreading centre (ELSC) in Tonga. Their work shows that back-arc spreading centres change even more rapidly than previously thought, suggesting that they are more active in capturing the subducted input from the mantle, and then rapidly releasing most of it when the spreading centre reaches a critical distance from the arc. Figure 3a of the paper (page 201) is a map of the region: the Tonga trench is the subduction zone's intersection with the surface; triangles on the Tonga ridge show the associated volcanic arc; and the location of the ELSC is marked.

The key ingredient in subduction zones is the mineralogically bound water that is carried into the mantle in the downgoing, subducted slab and then released into the overlying mantle wedge as the cold slab is heated. It promotes greater extents of mantle melting and the production of magmas that are progressively richer in silicon dioxide (SiO₂) and water.

1. Dickinson, E. *The Complete Poems of Emily Dickinson* (Little, Brown, 1924).
2. Williams, P. H. & Osborne, J. L. *Apidologie* **40**, 367–387 (2009).
3. Thorp, R. W. & Shepherd, M. D. in *Red List of Pollinator Insects of North America* CD-ROM Version 1 (eds Shepherd, M. D., Vaughan, D. M. & Black, S. H.) (Xerces Soc. Invertebrate Conserv., Portland, Oregon, 2005); www.xerces.org/Pollinator_Red_List/Bees/Bombus_Bombus.pdf
4. Cameron, S. A. et al. *Proc. Natl Acad. Sci. USA* doi:10.1073/pnas.1014743108 (2011).
5. Keesing, F. et al. *Nature* **468**, 647–654 (2010).
6. Stout, J. C. & Morales, C. L. *Apidologie* **40**, 388–409 (2009).
7. Vredenburg, V. T., Knapp, R. A., Tunstall, T. S. & Briggs, C. J. *Proc. Natl Acad. Sci. USA* **107**, 9689–9694 (2010).
8. Otterstatter, M. C. & Whidden, T. L. *Apidologie* **35**, 351–357 (2004).
9. Whitehorn, P. R., Tinsley, M. C., Brown, M. J. F., Darvill, B. & Goulson, D. *Proc. R. Soc. B* doi:10.1098/rspb.2010.1550 (2011).

ELSC provided by Dunn and Martinez¹ could improve the construction of these geodynamic models.

The authors' investigation¹ is part of the Ridge 2000 programme sponsored by the US National Science Foundation⁸. This is an interdisciplinary initiative to study Earth's oceanic spreading ridge system as an integrated whole, from its inception in the mantle to its manifestations in the biosphere and the water column. Intensive studies at three integrated study sites (including the ELSC) seek to establish links between different parts of these complex systems "from mantle to microbe". The ELSC was chosen as a site because of the gradational nature of the effects of subduction (especially of water) along its axis. Hydrous magma degassing and crustal composition control the composition of hydrothermal fluids⁹, and therefore also strongly influence the microfauna and macrofauna at hydrothermal vents along the spreading centre. In their work, Dunn and Martinez exploited the expected link between crustal properties and mantle-source composition.

Their research was made possible by the continually increasing investment in, and improvement of, ocean-bottom seismometers. Seismic-imaging studies use arrays of seismometers as receivers to provide a three-dimensional view of travelling seismic waves, whether fast or slow. The deployment of seismometers on the sea floor is not new. But this study¹ involved the largest, densest array of ocean-bottom seismometers deployed over an oceanic spreading centre anywhere on Earth, and permitted large-scale questions to be addressed at the ELSC.

Dunn and Martinez¹ used ship-borne airguns as the seismic-wave source to produce many relatively low-energy bursts that allowed the shallow crustal structure to be examined. Other seismic-imaging studies are under way with much longer deployments of the same seismometers, and using earthquake energy as a high-energy seismic-wave source to image the deeper mantle wedge and subducted slab. These investigations cover the same geographical area as the current shallow study, and may provide additional tests of the hypothesis of a critical distance in which volcanic-arc material is captured.

Further tests of the Dunn and Martinez hypothesis will be forthcoming. If, as required by the hypothesis, there is an excellent

This results in crust that is thicker, seismically slower and more porous. It is these changes that are observed, in both crustal properties² and rock composition³, southwards along the 'zero-age' axis of the ELSC, as the distance between the Tonga volcanic arc and the ELSC diminishes and the input of subducted materials to the back-arc increases.

By examining the crustal structure across the axis as well as along it, Dunn and Martinez¹ are peering back to a time when the back-arc basin was narrower. The volcanic morphology at the surface and the seismic velocities of the underlying few kilometres of crust show that, over a short period of time, as the back-arc spreading centre pushed itself away from the volcanic arc by sea-floor spreading, the volcanic crust abruptly became smoother, thinner, denser and probably less porous. In other words, it became less influenced by subducted water. These relatively shallow observations of the crust reflect what is happening in the deeper mantle wedge.

The abruptness of the changes is the crucial factor here, as it suggests that the spreading centre is doing more than merely sampling whatever mantle it passes over. It remains to be seen how the concept of active capturing of subduction-influenced mantle and its rapid release at a critical distance will influence the increasingly sophisticated models that have been proposed for the formation of magmas behind the volcanic arc^{4,5}. The conceptual cartoons that arise from these models of magma genesis are not yet sufficiently detailed. At the same time, geophysical imaging of the mantle wedge in other arcs⁶, and geodynamic models of the mantle wedge and slab that include dehydration and rheological changes⁷, are leading to more realistic models of subduction-zone processes and hint at a region in the mantle where conditions change rapidly over short distances. The time constraints from the