between these two forms lead to transfers of many electrons, which can drive oxidation or reduction reactions of the host rocks. Large tracts of deep crustal rocks exhibit evidence for in situ oxidation that may have been influenced by sulfur redox chemistry (7).

The assumption that sulfur in deep fluids exists chiefly as sulfide or sulfate is based on these species being the most common forms in surface waters, but they could also be products of rapid reactions of other sulfur compounds in deep fluids as they rise to the surface. Pokrovski and Dubrovinsky used a hydrothermal diamond-anvil cell and Raman spectroscopy to look for other sulfur species dissolved in water at high pressures and temperatures. They found that S_3^- is favored as temperature and pressure are increased, and predominates above ~300°C at all pressures investigated and over a wide pH range.

The results offer intriguing possibilities for rethinking processes in deep geofluids. They support additional pathways for gold transport and deposition in hydrothermal systems (8). They also require a new assessment of sulfur's history before it reaches the atmosphere in some volcanic eruptions. Sulfur-rich volcanic systems are associated with convergent plate boundaries—for example, the Pacific "Ring of Fire"—and may emit large volumes of SO_2 gas. So much stratospheric SO_2 was liberated during the 1991 eruption of Mount Pinatubo that average surface temperatures dropped globally by ~0.5°C for several years (9). Interestingly, more sulfur was degassed in that event than could be accounted for in the magma parent, and the simplest explanation is that a sulfur-rich vapor phase released deep below the volcano was carried upward with the rising magma and into the eruption plume (10). If Pokrovski and Dubrovinsky are correct, much of the SO_2 that caused temporary global cooling could have formed from precursory aqueous S_3^-.

If S_3^- is to predominate in fluids at depth, it must be stable in both acidic and alkaline solutions at high pressures and temperatures. As pressure and temperature increase, acids such as HCl and H_2SO_4 become much weaker and water dissociates more extensively to H^+ and OH^-. (Neutral pH in pure water at the pressures and temperatures encountered 15 km beneath an active mountain belt such as the Himalayas is about 4, rather than 7.) Elevated pressure also enhances the solubility of the minerals lining the fracture and cavity walls that allow fluids to migrate (11). Acids would have less capacity to neutralize alkaline solutions that are produced by a wide range of mineral-water reactions. Thus, it is noteworthy that the S_3^- anion was found to

be stable over a wide range of pH.

However, Pokrovski and Dubrovinsky provide only part of the story. In magmas and ore-forming fluids, iron content can influence the behavior of sulfur and its oxidation state, but only iron-free fluids were investigated. Pokrovski and Dubrovinsky suggest that the similarity of the 103° S–S–S bond angle in S_3^- to that of H–O–H might make it more easily accommodated into the tetrahedral hydrogen-bonded network of the aqueous solvent. However, other groups, also using in situ Raman spectroscopy, detected no evidence for hydrogen bonding in water above ~400°C (12, 13); such results imply that this familiar and chemically important feature of water diminishes with temperature.

If we could shine light on deep geologic fluids, the apparent prevalence of S_3^- means that they should be ultramarine blue in color (14). Pokrovski and Dubrovinsky have now done for deep fluids what others have done for silicate glasses and precursors to volcanic gases (15, 16) by revealing a form of sulfur with an intermediate redox state (relative to sulfide and sulfate) whose geochemical consequences must now be explored. Their findings continue a tradition of surprises in sulfur

geochemistry that extends even to the source of color in ultramarine pigment, which could involve S_2^- in addition to S_3^- (17).

References

1. W. C. Brögger, H. Bäckström, *Z. Kristallogr.* **18**, 231 (1891).
2. V. P. Belichenko, V. V. Mazykin, A. N. Platonov, A. N. Tarashchan, *Akad. Nauk. Ukr. RSR Ser. B* **35**, 99 (1973).
3. G. S. Pokrovski, L. Dubrovinsky, *Science* **331**, 1052 (2011).
4. C. W. Mandeville, *Elements* **6**, 75 (2010).
5. T. M. Seward, *Econ. Geol. Monogr.* **6**, 398 (1989).
6. J. W. Hedenquist, J. B. Lowenstern, *Nature* **370**, 519 (1994).
7. R. C. Newton, C. E. Manning, *J. Petrol.* **46**, 701 (2005).
8. G. S. Pokrovski, B. R. Tagirov, J. Schott, J.-L. Hazemann, O. Proux, *Geochim. Cosmochim. Acta* **73**, 5406 (2009).
9. M. P. McCormick, L. W. Thomason, C. R. Trepte, *Nature* **373**, 399 (1995).
10. K. Hattori, *Geology* **21**, 1083 (1993).
11. D. Dolejs, C. E. Manning, *Geofluids* **10**, 20 (2010).
12. W. Kohl, H. A. Lindner, E. U. Franck, *Ber. Bunsenges. Phys. Chem.* **95**, 1586 (1991).
13. J. D. Frantz, J. Dubessy, B. Mysen, *Chem. Geol.* **106**, 9 (1993).
14. W. F. Giggenbach, *Inorg. Chem.* **10**, 1306 (1971).
15. N. Métrich, A. J. Berry, H. S. C. O'Neill, J. Susini, *Geochim. Cosmochim. Acta* **73**, 2382 (2009).
16. B. Binder, H. Keppler, *Earth Planet. Sci. Lett.* **301**, 190 (2011).
17. R. J. H. Clark, M. L. Franks, *Chem. Phys. Lett.* **34**, 69 (1975).

ECOLOGY

Functional Extinctions of Bird Pollinators Cause Plant Declines

Cagan H. Sekercioglu

Researchers have documented how the loss of pollinating birds affects a plant that depends on them.

The world's approximately 10,000 bird species are key "mobile links" (1) in most major ecosystems, from tropical rainforests to the depths of the Antarctic Ocean. Birds provide crucial ecosystem services, including seed dispersal, pollination, predation, scavenging, nutrient deposition, and ecosystem engineering (2–4). Countless plant species depend on mutualistic relationships with birds for their survival (5–7). However, threats such as habitat loss, introduced species, and exploitation (7–9), exacerbated by the growing impact of climate change (10, 11), are causing large population declines and extinctions among birds (see the photo). As a result, hundreds of species now contribute negligibly to ecosystem function

and are "functionally extinct" (8). Researchers have speculated that these losses could lead to declines in dependent plants (12–14), but experimental proof has been scarce (4, 7, 12). On page 1068 of this issue, however, Anderson et al. (6) show that the functional extinction of three kinds of pollinating birds on an island in New Zealand has reduced pollination, seed production, and plant density in a dependent shrub.

Although research on bird-plant mutualisms tends to focus on seed dispersal rather than on pollination (5), researchers have documented about 2000 bird species visiting flowers; more than 900 species pollinate about 500 of the 13,500 genera of vascular plants (7, 15, 16). Anderson et al. studied three species of birds known to pollinate the shrub *Rhabdothamnus solandri*. They compared shrub populations at sites on the North

Department of Biology, University of Utah, Salt Lake City, UT 84105, USA. E-mail: c.s@utah.edu
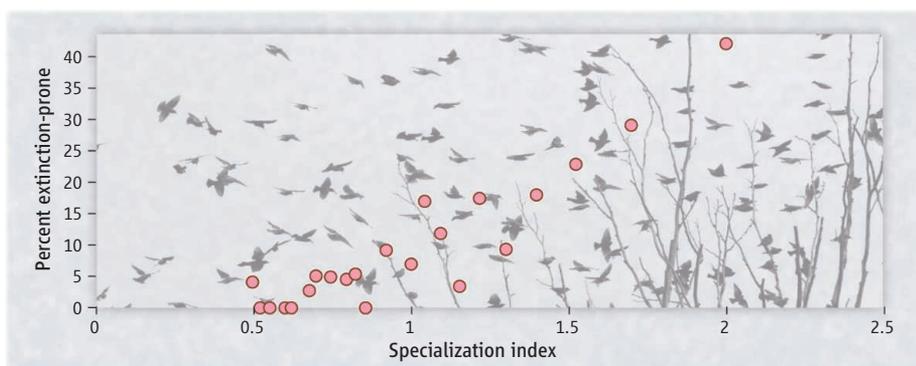
Special vulnerability. Bird species with greater food and habitat specialization (to the right on *x* axis) face greater extinction risk. Birds that pollinate plants are expected to be especially vulnerable. Specialization index = log [100/(number of habitats used × number of food types eaten)]. Graph is based on all bird species in the world (*8*).

Island of New Zealand, where the birds are functionally extinct, to populations at sites on three nearby islands, where the birds remain abundant. Combining field studies with experiments, the authors showed that functional extinction of the birds limited pollination of the shrub, reducing seed production by 84% and reducing the number of juvenile plants produced per adult by 55%.

This report stands out because of its exceptional consideration of the long-term demographic effects of pollination failure. Anderson *et al.* followed the plant populations from pollination to seed production to recruitment, and then bolstered their findings with "seed addition" experiments. In these experiments, the authors added shrub seeds to plots on the island where the pollinating birds were functionally extinct, then tracked the resulting seedlings for 5 years. Seedling densities increased in the plots, providing evidence that pollination reduction (and not other factors) explained the shrub's decline. Seed addition is a time-consuming and labor-intensive approach, but it needs to be widely applied in other ecosystems.

The conservation implications of Anderson *et al.*'s findings are profound. Reduced recruitment resulted in gradual population decline. Such gradual, cascading effects of pollination failure may be far more common than has been realized. This issue is more urgent than ever because of widespread pollinator

declines (*12*) and projected extinctions that may make pollinators the most threatened bird functional group in the 21st century (*8*). Increased specialization increases extinction risk (see the figure), and higher extinction rates of specialized pollinators will result in additional knock-on extinctions of dependent species (*17*).

Birds are particularly important pollinators for sparsely distributed plant species with isolated populations (*18*). Functional extinctions of birds (*7, 8, 12*) already may have triggered declines in these species, but conclusive studies are absent. This is particularly true in understudied tropical forests where seed dispersal and pollination by birds are particularly common, most plants are sparsely distributed, and the majority of the world's threatened bird species reside (*7*).

Anderson *et al.* also highlight the importance of avian pollinators on islands—and the importance of protecting them from threats such as introduced species. On Guam, another Pacific island, many avian pollinators have been wiped out by the introduced brown treesnake (*Boiga irregularis*), resulting in reduced seed set for the tree *Erythrina variegata* var. *orientalis* and reduced seed set and recruitment for the tree *Bruguiera gymnorrhiza.* In contrast, nearby snake-free Saipan has retained an intact pollinator community (*13*).

Avian pollination is especially important in Australia, New Zealand, and other Pacific Ocean islands, which have greater proportions of bird-pollinated plants than other

islands (*18*). Oceanic islands such as Guam and New Zealand are particularly vulnerable to pollinator losses (*7, 13, 14, 19*) due to tighter mutualisms among fewer species and the vulnerability of "naïve" residents to introduced predators—the main drivers of the declines and extinctions of oceanic island birds (*6, 7*). Pollinator losses particularly endanger island plants because many have lost their ability to self-pollinate and are entirely dependent on endemic pollinators (*19*).

Another cause for concern is that bird pollination often involves fewer, more obligate species than avian seed dispersal, and plants are more likely to be limited by a shortage of bird pollinators than by a lack of dispersers (*5*). Most plant populations investigated show pollinator limitation, and pollinator declines also reduce agricultural yields (*12*). Birds are believed to pollinate 3.5 to 5.4% of 1500 species of crop or medicinal plants, three-quarters of which cannot self-pollinate (*15*).

There is still time to conserve most of the world's birds and their mutualists, but last-minute efforts to hold extinctions at bay are not sufficient. Governments, nongovernmental organizations, and the public must immediately focus on stopping population declines and maintaining ecosystem functions and services (*20*), and ecologists need to follow the lead of Anderson *et al.* and conduct the long-term studies needed to understand, quantify, and communicate the consequences of functional extinctions.

References and Notes
1. J. Lundberg, F. Moberg, *Ecosystems* **6**, 87 (2003).
2. C. H. Sekercioglu, *Trends Ecol. Evol.* **21**, 464 (2006).
3. C. J. Whelan *et al.*, *Ann. N.Y. Acad. Sci.* **1134**, 25 (2008).
4. D. G. Wenny *et al.*, *Auk* **128**, 1 (2011).
5. D. Kelly *et al.*, *N.Z. J. Bot.* **42**, 89 (2004).
6. S. H. Anderson, D. Kelly, J. J. Ladley, S. Molloy, J. Terry, *Science* **331**, 1068 (2011); 10.1126/science.1199092.
7. N. S. Sodhi, C. H. Sekercioglu, J. Barlow, S. K. Robinson, *Conservation of Tropical Birds* (Wiley, Oxford, 2011).
8. C. H. Sekercioglu, G. C. Daily, P. R. Ehrlich, *Proc. Natl. Acad. Sci. U.S.A.* **101**, 18042 (2004).
9. S. H. M. Butchart *et al.*, *Science* **328**, 1164 (2010).
10. C. H. Sekercioglu *et al.*, *Conserv. Biol.* **22**, 140 (2008).
11. J. Wormworth, C. H. Sekercioglu, *Winged Sentinels: Birds and Climate Change* (Cambridge Univ. Press, Port Melbourne, 2011).
12. S. G. Potts *et al.*, *Trends Ecol. Evol.* **25**, 345 (2010).
13. H. S. Mortensen *et al.*, *Biol. Conserv.* **141**, 2146 (2008).
14. J. J. Ladley, D. Kelly, *Nature* **378**, 766 (1995).
15. G. P. Nabhan, S. L. Buchmann, in *Nature's Services*, G. Daily, Ed. (Island, Washington, DC, 1997), pp. 133–150.
16. S. S. Renner, in *Plant-Pollinator Interactions: From Specialization to Generalization*, N. M. Waser, J. Ollerton, Eds. (Univ. of Chicago Press, Chicago, 2005), pp. 123–144.
17. R. R. Dunn *et al.*, *Proc. Biol. Sci.* **276**, 3037 (2009).
18. H. A. Ford, *Proc. Ecol. Soc. Australia* **14**, 153 (1985).
19. P. A. Cox, T. Elmqvist, *Conserv. Biol.* **14**, 1237 (2000).
20. C. H. Sekercioglu, in *Conservation Biology for All*, N. S. Sodhi, P. R. Ehrlich, Eds. (Oxford Univ. Press, Oxford, 2010), pp. 45–72.
21. I thank S. Anderson, D. Kelly, D. Wenny, C. Whelan, and T. Williams for their helpful comments.

At risk. Venezuela's endangered scissor-tailed hummingbird (*Hylonympha macrocerca*) is just one pollinator under threat.

10.1126/science.1202389