

the classical form of the model? Is EMD output modulated by behavioral state or by corollary discharge, such as might occur during voluntary changes in gaze? In flies, the itemized network of neurons and synaptic connections for EMDs and those regions devoted to decoding and integrating EMD output comprise only a fraction of the visual circuitry of the optic lobes identified to date. What functions do the vast majority of visual processes provide? And how do these processes interact with the signals for self-motion generated by the EMD?

Finally, are there other elementary detector schemes for different sensory modalities? The powerful combination of *Drosophila* neurogenetics and molecular biology, coupled with rapidly evolving technologies for tracking and manipulating complex visual behavior, is providing an exceptionally clear view on the cellular, cell circuit, and behavioral levels of organization for the elementary motion detector and beyond.

Where can I find out more?

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White-Nose Syndrome fungus introduced from Europe to North America

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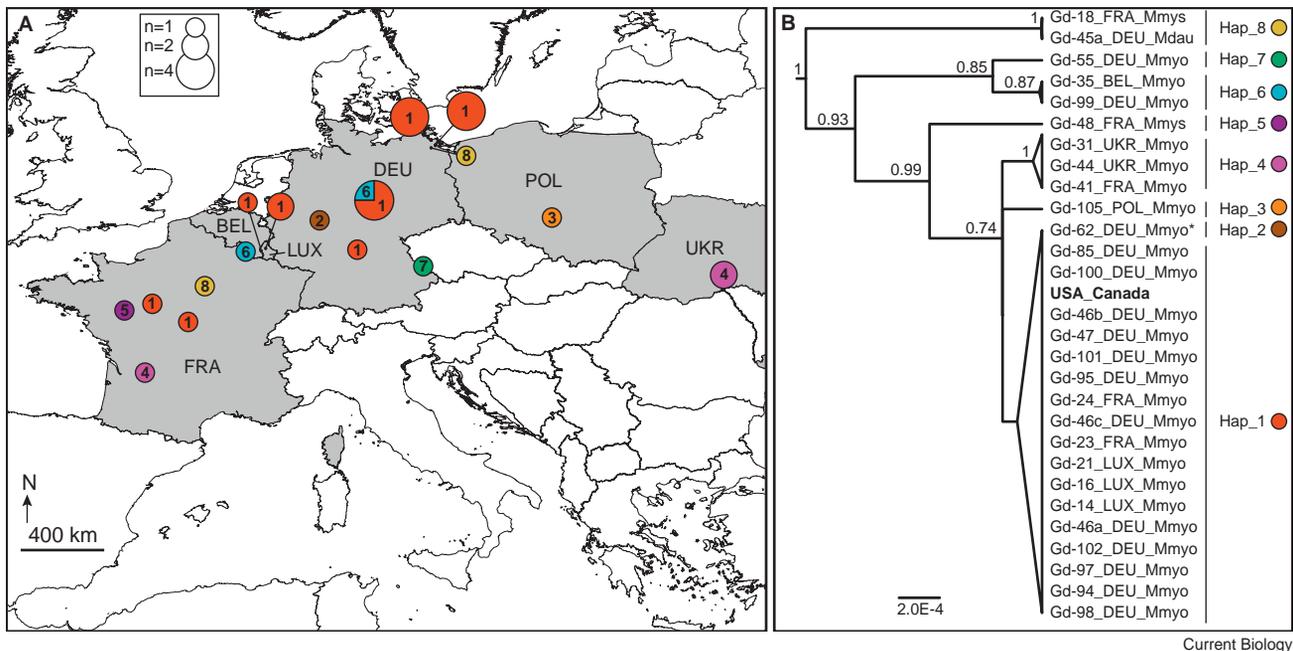
The investigation of factors underlying the emergence of fungal diseases in wildlife has gained significance as a consequence of drastic declines in amphibians, where the fungus *Batrachochytrium dendrobatidis* has caused the greatest disease-driven loss of biodiversity ever documented [1]. Identification of the causative agent and its origin (native versus introduced) is a crucial step in understanding and controlling a disease [2]. Whereas genetic studies on the origin of *B. dendrobatidis* have illuminated the mechanisms behind the global emergence of amphibian chytridiomycosis [3], the origin of another recently-emerged fungal disease, White-Nose Syndrome (WNS) and its causative agent, *Pseudogymnoascus destructans*, remains unresolved [2,4]. WNS is decimating multiple North American bat species with an estimated death toll reaching 5–6 million. Here, we present the first informative molecular comparison between isolates from North America and Europe and provide strong evidence for the long-term presence of the fungus in Europe and a recent introduction into North America. Our results further demonstrate great genetic similarity between the North American and some European fungal populations, indicating the likely source population for this introduction from Europe.

Diversity among genetic markers is a powerful tool to reconstruct colonisation events and exchanges between populations [5]. Populations in recently colonised areas harbour genetic signatures distinct from long established ones (for example, [5]). We therefore used genetic data to test if *P. destructans* is long established in Europe (that is, native) and assess whether it

is a likely source population for the recent introduction to North America. Twenty-eight *P. destructans* isolates, collected from *Myotis* bats over a five-year timeframe and covering regions in Europe with the highest number of reported cases of *P. destructans* infection [6] (Figure 1A), were sequenced at eight genomic loci and combined with published data from seventy-one North American isolates covering a similar range and timeframe [4,7] (see Supplemental Experimental Procedures).

Seven of the eight genes sequenced were polymorphic among the European isolates (Tables S1 and S2), sharply contrasting with the absence of variation observed across the North American isolates [4,7]. These data demonstrate the older origin of the European population of *P. destructans* compared with that of the North American population. The number of isolates sequenced was larger in North America (n=71) than Europe (n=28), likely leading to an under-estimate of the number of haplotypes present in Europe. Photographic evidence has suggested the presence of *P. destructans* in Europe for decades without any associated mass mortality, consistent with an endemic European distribution and host-pathogen co-evolution [2,6,8], although such data did not inform on the presence of the fungus in Europe over longer timeframes.

Combining the gene fragments for each isolate allowed the detection of eight haplotypes across Europe, and the most common (Hap_1) was shared with all North American isolates (Figure 1). Hap_1 was found in Western but not Eastern Europe (Figure 1A). Phylogenetic reconstruction identified samples from France, Germany and Belgium as the most basal (Figure 1B). The absence of genetic variability at these eight loci in North American isolates suggested either novel appearance in the area [4,7] or recent emergence of a virulent strain of a previously benign fungus not necessarily present on bats [2]. The fact that the most common European haplotype is 100% identical at the sampled loci to the clonal haplotype from North America corroborates a recent inter-continental fungal transfer from Europe to North America [6], rather than the emergence of a virulent strain



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Figure 1. Spatial distribution and relationship between the *Pseudogymnoascus destructans* haplotypes.

(A) Distribution of the eight haplotypes of *Pseudogymnoascus destructans* among sampling locations. Haplotypes are indicated per hibernacula both with colours and by their respective numbers (matching panel B). Pie charts are drawn proportional to the number of samples analyzed per location: where more than one haplotype was detected in a location, a pie chart is displayed to indicate the proportion of each haplotype. (B) Bayesian phylogenetic tree inferred from the concatenation of eight gene fragments (total of 5,170 nt), constructed using BEAST and rooted with *P. pannorum* (see Supplemental Information). Bayesian posterior probability values are shown near each supported node (>0.7). The sole haplotype found in the Eastern US and Canada is shown in boldface. Identical sequences were collapsed (appearing as 'triangles'). The scale bar indicates nucleotide substitutions per site. Tip labels are composed of the isolate culture name (Gd-xxx), followed by the 3-letter ISO code of the isolate country of origin (FRA, France; BEL, Belgium; DEU, Germany; LUX, Luxembourg; POL, Poland; UKR, Ukraine) and the abbreviated name of the bat species from which the culture was isolated (Mdau, *Myotis daubentonii*; Mmyo, *Myotis myotis*; Mmys, *Myotis mystacinus*). *The sequence from isolate Gd-62 harboured a unique haplotype but since this resulted from an indel (not considered here as a phylogenetic character), it does not appear unique in this tree. Haplotype numbers and colours (matching panel A) are also represented. See also Tables S1 and S2 in the Supplemental Information.

in North America. The recent transfer scenario is fully consistent with results from inoculation experiments showing no significant difference in virulence between European and American isolates [9]. Although a larger sample size and geographic coverage would be required to be conclusive, the haplotype shared between North American and European isolates appears to be unevenly distributed within Europe, suggesting Western Europe as the most likely origin for North American *P. destructans*. We cannot exclude an Eastern Palearctic origin, although this seems unlikely based on our genetic data.

A recent study characterized a heterothallic mating system in *P. destructans* with two mating types present in Europe [10], indicating capacity for sexual recombination. Although we did not detect recombination in our data set (Supplemental Information), the hypothesis remains valid since the number of parsimony-informative sites in our data set was limited,

making the power to detect recombination low, and also the predominant mode of reproduction could be clonal.

As expected, the genetic markers used were more variable and informative than the highly conserved internal-transcribed spacer or small-subunit sequences used previously [6] and provided improved insight into phylogenetic relationships between isolates from both continents. Nonetheless, we expect that the survey of more markers, such as microsatellites, or whole genome sequencing and further sampling would provide additional phylogenetic resolution and a more precise identification of the European origin of the North American *P. destructans*.

In conclusion, our findings provide the first strong evidence for a long-term presence of *P. destructans* in Europe and a recent introduction from the Western Palearctic into North America, leading to the emergence of WNS. This scenario would explain the lack of associated

mass mortality among European bats while the naive North American populations are collapsing. We argue that understanding how European bat species interact with the fungus without apparent adverse health effects holds the key to a better understanding of mammalian responses to fungal pathogens. Additionally, given that there is no bat migration between North America and Europe, it is very likely that the fungus has been introduced to North America via anthropogenic activities, highlighting once more the critical need for the application of tighter control of international transfer and trade in biological material [1,2].

Supplemental Information

Supplemental Information includes experimental procedures and two data tables, and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.01.047>.

Acknowledgments

Funding came from the Royal Veterinary College/Zoological Society of London,

the British Veterinary Zoological Society and Bat Conservation International.

Acknowledgments to Tony Sainsbury, Michael Waters, Marcus Fritze and sample contributors for their practical assistance, and to Eric Petit and Serena Dool for comments.

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Opportunities and costs for preventing vertebrate extinctions

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Despite an increase in policy and management responses to the global biodiversity crisis, implementation of the 20 Aichi Biodiversity Targets still shows insufficient progress [1]. These targets, strategic goals defined by the United Nations Convention on Biological Diversity (CBD), address major causes of biodiversity loss in part by establishing protected areas (Target 11) and preventing species extinctions (Target 12). To achieve this, increased interventions will be required for a large number of sites and species. The Alliance for Zero Extinction (AZE) [2], a consortium of conservation-oriented organisations that aims to protect Critically Endangered and Endangered species restricted to single sites, has identified 920 species of mammals, birds, amphibians, reptiles, conifers and reef-building corals in 588 ‘trigger’ sites [3]. These are arguably the most irreplaceable category of important biodiversity conservation sites. Protected area coverage of AZE sites is a key indicator of progress towards Target 11 [1]. Moreover, effective conservation of AZE sites is essential to achieve Target 12, as the loss of any of these sites would certainly result in the global extinction of at least one species [2]. However, averting human-induced species extinctions within AZE sites requires enhanced planning tools to increase the chances of success [3]. Here, we assess the potential for ensuring the long-term conservation of AZE vertebrate species (157 mammals, 165 birds, 17 reptiles and 502 amphibians) by calculating a conservation opportunity index (COI) for each species. The COI encompasses a set of measurable indicators that quantify the possibility of achieving successful

conservation of a species in its natural habitat (COI_h) and by establishing insurance populations in zoos (COI_c).

COI_h considered costs of land acquisition and management in the species’ range country [4], likelihood of political instability and/or politically motivated violence (including terrorism) affecting conservation operations on the ground, as well as the latent impact of urban expansion on the species’ natural habitat (Supplemental information). Global distribution of the COI_h for all AZE vertebrates is shown in Figure S1 (Supplemental information). COI_c included costs of managing a zoo population of at least 500 individuals of a species [5], together with a measure of breeding expertise available for AZE vertebrates in zoos in the International Species Information System [6] or, for amphibians, bred in Amphibian Ark programs [7]. Although reintroduction costs are also important to consider, we did not include these because of a lack of adequate data.

Conservation opportunities for AZE vertebrates in their natural habitat were high, given that ~39% of species had high COI_h (maximum = 10) values (Figure 1A). Mean (± SD) COI_h for all species was 6.22 ± 1.80 (reptiles (6.89 ± 1.64), mammals (6.46 ± 1.79), amphibians (6.19 ± 1.70) and birds (6.03 ± 2.07)). Opportunities for management in zoos were low for all taxonomic groups (Figure 1A). Mean COI_c for all species was 2.79 ± 2.88 (maximum = 10) (reptiles (7.06 ± 4.70), birds (3.03 ± 3.01), amphibians (2.69 ± 2.72) and mammals (2.39 ± 2.64)). Overall, 15 species had a high COI_h and COI_c, and another 15 a low COI_h and COI_c.

Total annual costs for effectively managing all AZE vertebrates in their natural habitat were US\$ 1.18 billion (Supplemental information). AZE site costs (per species and year) were lowest for reptiles (US\$0.59 ± 0.65 × 10⁶), followed by mammals (US\$0.95 ± 1.52 × 10⁶), amphibians (US\$1.20 ± 1.91 × 10⁶) and birds (US\$2.53 ± 4.74 × 10⁶). These differences were largely due to variations in total annual costs of managing existing protected areas in the more expensive developed countries than in developing nations [4]. By region, estimated AZE site costs were highest for South America and lowest for northern Africa (Figure 1B). Total annual costs for effectively managing all AZE vertebrates in zoos were US\$0.16 billion (Supplemental