Invited reply

Deforestation and tropical insect extinctions

In a study comparing historical and recent records of forest-dwelling *Helictopleurus* dung beetles across Madagascar, Hanski *et al.* (2007) reported that species not found in Madagascar-wide sampling in 2002–2006 have experienced a significantly higher level of deforestation within their known geographical ranges than those species that were recorded. They suggested that deforestation is responsible for the apparent extinction of the former species. Rös & Pineda (2009) observed that the data in Hanski *et al.* (2007) are not sufficient to draw definite conclusions about extinctions because recent sampling was not conducted at many of the localities where the apparently extinct species had been formerly collected, mostly more than 50 years ago.

We agree with Rös & Pineda (2009): many of the apparently extinct species are probably not (yet) truly extinct, though they may have declined to low abundance. It is practically impossible to conclusively prove the extinction of a beetle species within such a large area as Madagascar. Nonetheless, given the great importance of understanding the processes and rates of species extinctions, especially in tropical forests (Whitmore & Sayer 1992), analyses based on indirect evidence, such as association with regional deforestation, can be informative (Brooks *et al.* 2002). Hanski *et al.* (2007) included in their analysis as a covariate the average distance between historical localities for each species and the recent sampling localities, which goes some way to alleviate the problem that many of the historical localities could not be resampled (Rös & Pineda 2009). The vast majority of forest-dwelling *Helictopleurus* are strictly confined to their native habitat (Wirta *et al.* 2008), and only four species have made the shift to the abundant new resource of cattle dung in open and semi-open habitats (Hanski *et al.* 2008; Rahagalala *et al.* 2009).

The veritable hot spot of *Helictopleurus* species richness is northeastern Madagascar (figure 1a), with 10 historical localities for the apparently extinct species in Hanski *et al.* (2007) within an area of 150 × 300 km (see fig. 1b in Rös & Pineda 2009). We have conducted field studies in this region in 2007–2008, in the Marojejy National Park and in the Anjanaharibe-Sud Special Reserve, which represent some of the largest remaining intact forest

areas in Madagascar. The total sample size is 909 individuals, with an asymptotic species number of 13 (figure 1b), amounting to 34 per cent of all the *Helictopleurus* species that have been sampled since 2002.

Of the 13 species, 1 is undescribed (O. Montreuil 2009, personal communication) and 4 were classified as apparently extinct by Hanski *et al.* (2007): *furcicornis*, *nigricans*, *undatus* and *vadoni*, which have now been sampled for the first time in 30–50 years. That so many ‘apparently extinct’ species were rediscovered justifies the criticism by Rös & Pineda (2009) and shows that this part of Madagascar had remained poorly sampled. However, up-dating the database of Hanski *et al.* (2007) with these rediscoveries leaves the previous conclusions unchanged.

First, three of the four newly rediscovered species were among the best candidates to be rediscovered owing to their past commonness and relatively low level of deforestation (50–60% in the past 50 years) within their geographical ranges (figure 1c). Second, in spite of the large sample size (figure 1b), nine species that have formerly occurred in this part of Madagascar remained unrecorded, many of them collected in the coastal areas that are now nearly completely deforested. Third, a logistic regression model for the revised set of apparently extinct species shows that species not sampled in 2002–2009 are among the historically uncommon species and have experienced a high level of deforestation within their ranges (table 1). The model fits the revised data better ($p = 0.84$) than the original data ($p = 0.38$; Hanski *et al.* 2007). And fourth, in the revised dataset there is a significant effect of body size on the status of the species, larger species having a greater probability of being apparently extinct than smaller species (table 1, figure 1d). Large species are generally more dependent than small ones on the dung of large-bodied lemurs (Wirta *et al.* 2008), and the effect of body size in table 1 is likely to reflect the regional decline of especially large-bodied lemurs owing to deforestation, habitat degradation and hunting.

Madagascar is a priority region for conservation owing to the exceptionally high level of endemism of its fauna and flora, the sizes of which are still underestimated (Vieites *et al.* 2009). Ecological theory and empirical studies indicate that the long-term viability of populations and species is threatened by habitat loss and fragmentation (Hanski 2005), but it is difficult to demonstrate such effects directly for species other than birds (Robinson 1999; Sekercioglu *et al.* 2002) and other highly detectable taxa on small spatial scales. We maintain that the association between the historically documented deforestation within the geographical range of each species and the status of the species in extensive surveys, whether recorded or apparently extinct, is indicative of serious threat.

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Figure 1. (a) A map of regional species richness of *Helictopleurus* in Madagascar. The shading indicates the number of species recorded from each cell. There is much regional variation in sampling effort, but the results indicate high species richness in the Masoala peninsula and forest areas to its west and north. Light shade, 1–5; light grey, 6–11; dark grey, 12–17; black, 18–21. (b) Species-accumulation curve for samples collected in the Marojejy NP in November–December 2007 and in the Anjanaharibe-Sud Special Reserve in November–December 2008. Sampling was conducted with a range of bait types in forests at elevations from 200 to 2000 m above sea level. Total sampling effort was 1812 trap-nights. The samples were aggregated by sampling date and were added to the graph in random order. (c) The plot shows whether a species was collected by Hanski *et al.* (2007) (open symbol), discovered by us in 2007–2008 (open triangle), or remains ‘apparently extinct’ (closed symbol), in relation to the relative forest loss within the range of the species and its past commonness (these variables were calculated as in Hanski *et al.* 2007). (d) As (c), but the vertical axis shows the body size of the species (length in mm).

Table 1. Stepwise logistic regression model explaining whether a species of *Helictopleurus* has been sampled ($n = 33$) or not ($n = 17$) in 2002–2009 (p -value for the full model = 0.84; d.f. 45).

explanatory variable	deviance	difference	p
constant	64.10		
past commonness	51.71	12.39	0.0004
relative forest loss	45.27	6.44	0.011
distance to our traps	39.69	5.58	0.018
body size	35.76	3.93	0.048

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