What determines whether a species of insect is described? Evidence from a study of tropical forest beetles

NIGEL E. STORK,1 PETER S. GRIMBACHER,1 ROSS STOREY,2 ROLF G. OBERPRIELER,3 CHRIS REID4 and S. ADAM SLIPINSKI3
1School of Resource Management and Geography, University of Melbourne, Richmond, Melbourne, Vic., Australia, 2Department of Primary Industries & Fisheries, Qld, Australia, 3Australian National Insect Collection, CSIRO Entomology, Canberra, Australia, 4Australian Museum, Sydney, NSW, Australia

Abstract. 1. The rainforest canopy has been called ‘the last biological frontier’, and if this is true, there should be more undescribed species in this stratum than the ground stratum.

2. Here, we test this and other hypotheses regarding traits of described and undescribed species by a sub-sample of 156 species into 96 described and 60 undescribed species from a beetle assemblage of 1473 species collected from the canopy and ground in an Australian lowland rainforest.

3. We show that described species are significantly more likely to be in the canopy, are more likely to be larger and, if they are large, are more likely to have been described earlier.

4. Undescribed species are just as likely to be found near the ground as in the canopy and are more likely to be smaller.

5. After the first year of sampling, ‘new’ described and undescribed species not previously encountered continued to appear in each of three further years of trapping.

6. These data show that the canopy fauna is in fact relatively ‘well known’, and that the undescribed species to be found in both strata are likely to be smaller than described species and are less likely to be plant feeders.

Key words. Coleoptera, rainforest canopy, species traits, tropical insects, undescribed species.

Introduction

Estimates of how many species of insects there are on Earth vary from 3 million to 30 million (Erwin, 1982; Hodgkinson & Casson, 1991) but most commentators support a figure of around 5–12 million and agree that many of the undescribed species are to be found in tropical rainforests (Stork, 1993, 1999; Hammond, 1995; May, 2000; Ødegaard, 2000; Novotný et al., 2002). If these latter estimates are correct, then, since only about 720 000–950 000 species of insects have so far been described (Stork, 1993, 1999; Hammond, 1995), there remain another 75–90% to be discovered and described. In order to understand why some species are described and others are not described and to determine what these remaining undescribed species might be like, a number of studies that have examined correlates of the year species were described. Body size is a key variable for year of description for British beetles (Gaston, 1991), North American butterflies (Gaston et al., 1995), South American oscine passerine birds (Blackburn & Gaston, 1995), North American reptiles and amphibians (Reed & Boback, 2002) and Brazilian Cerrado anurans (Diniz-Filho et al., 2005) but not for Australian and Western European scarab beetles (Allsopp, 1997; Cabrero-Sañudo & Lobo, 2003) (see also Siemann et al., 1996). In addition, for parasites such as helminths and fleas, those species that have more hosts have been described earlier (Krasnov et al., 2005; Poulin & Mouillot, 2005). It would appear that most undescribed species are small, narrowly distributed and (where relevant) have narrow host ranges (Blackburn & Gaston, 1995; Gaston et al., 1995; Allsopp, 1997; Collen et al., 2004; Diniz-Filho et al., 2005; Krasnov et al., 2005; Baselga et al., 2007; Jimenez-Valverde & Ortúñ, 2007).
For insects, there has been some debate as to where, geographically speaking and habitat-wise, most undescribed species are to be found. A number of authors (Cabero-Sañudo & Lobo, 2003; Baselga et al., 2007; Jimenez-Valverde & Ortuño, 2007) looking at factors that related to year of description, found evidence that suggested that new species of several groups of Western Palearctic beetles were most likely to be discovered in the southern and eastern parts of this bioregion. Erwin (1982), in his estimation that there are 30 million species of tropical insects, suggested that two-thirds of these are in the canopy. He later described the rainforest canopy as the ‘last biological frontier’ (Erwin, 1983). Hammond et al. (1997) refuted this and suggested that the ratio of canopy to ground species was 1:5. In support of this argument, Jimenez-Valverde and Ortuño (2007) suggested that most new species of Carabidae in the Iberian Peninsula are likely to be hypogean (underground) species. A recent paper examining tropical forest beetle assemblages (Stork & Grimbacher, 2006) confirmed the findings of other authors working on different insect groups (Longino & Nadkarni, 1990; Basset et al., 1992, 2001; Devries et al., 1997; Rogers & Kitching, 1998; Brühl et al., 1998; Devries & Walla, 2001; Schultz et al., 2001; Tanabe, 2002; Charles & Basset, 2005) that there is strong vertical stratification in tropical forests. Stork and Grimbacher (2006) found that there was an almost equal proportion of canopy and ground specialists, about 25% in each case, with the remainder shared between these strata. The unanswered question is whether these strata are home to equal numbers of new species.

In this study, we take a new approach to this problem by examining samples of beetles from a tropical forest and determining which species have yet to be described. Here, we use part of a large rainforest beetle data set (Stork & Grimbacher, 2006; Grimbacher & Stork, 2007) containing 29 986 individuals and 1473 species, sampled equally from the canopy and the ground of a lowland rainforest in north-east Australia over a 4-year period.

We test two hypotheses: one concerned with which stratum, canopy or ground, is likely to contain the greater number of new species; and the other associated with which traits determine whether a species is more likely to have been described or not. First, since the canopy has been more difficult to access than ground-based habitats (Lowman & Nadkarni, 1995), we predict that there should be more undescribed species in the canopy. Second, we test the hypothesis that smaller species would have received less attention from collectors and taxonomists and therefore contain a higher proportion of undescribed species.

Methods

This study was conducted in continuous complex mesophyll vine forest at the Australian Canopy Crane research facility (16°17'S, 145°29'E), 3–4 km south-west of Cape Tribulation Queensland, Australia (Stork, 2007a). Beetles were sampled using a combined malaise and flight intercept trap (FIT) housed within an aluminium frame, with collecting trays placed at the bottom of the central net of the malaise trap (see Stork & Grimbacher, 2006 for details). There were five trapping locations, 40–60 m apart from each other. At each location, one trap was located on the ground and another was suspended from the crown of a tree 15–20 m above the ground in the canopy. Traps were run for 2 weeks almost every month from March 2000 to February 2004, resulting in 45 temporal samples, each consisting of five canopy FIT, five canopy malaise, five ground FIT and five ground malaise samples. To simplify analyses, in this study, we took cumulative sums of the whole sampling period and each trapping method.

Adult beetles were identified to family or subfamily according to Lawrence et al. (2000) and sorted to morphospecies. Beetle families and subfamilies were allocated to five feeding guilds: predators, herbivores, xylophages, fungivores and saprophages (see Grimbacher & Stork, 2007). We considered that variation in beetle body length between species was much greater, and more important, than the variation within species, and hence, for each species we measured the length of one medium-size individual using a calibrated graticule.

For those families or subfamilies of beetles where we had taxonomic expertise, we selected genera or groups of species where we could determine which species had been described or were undescribed. We noted that some species had been previously collected elsewhere and identified as new species in the Australian National Insect Collection or other museums but had not been described. The families (and sub-families) of beetles we examined were Chrysomelidae, Carabidae, Cleridae, Coccinellidae, Curculionidae, Dermentidae, Discolomatidae, Endomychidae, Erotylidae, Histeridae subf. Chlamydopsinae, Latridiidae, Pitidactylidae, Salpingidae, Scarabaeidae (excluding Melolonthinae), Scartiptidae, Silvanidae, Tenebrionidae.

To see how representative our taxonomic subset was, the canopy-to-ground ratio of analysed (described and undescribed) species and the remaining unanalysed species (remainder) were compared with a one-way ANOVA using traps as replicates (n = 5) with log-transformed count data, to conform to assumptions of normality. The canopy-to-ground ratio of captured individuals was also compared using this protocol.

We compared the number of described species caught in the canopy with those caught near the ground with a one-way ANOVA, using traps as replicates (n = 5) with square root-transformed count data. The number of undescribed species was also tested in this manner. The mean body size of species classified as described, undescribed and the remaining unanalysed species (remainder) caught from the canopy and the ground was tested with a two-way ANOVA, using traps as replicates (n = 5) with log-transformed data. The proportion of plant feeders (herbivores and xylophages) was compared in a similar fashion. For this analysis, family-guild allocations were sourced from Grimbacher and Stork (2007). For the described species, the relationship between body size and year of description was tested with linear regression using log-transformed body size data to conform to assumptions of normality and homogeneity of variances. The data in all figures were back-transformed from the means and standard errors (SE) used in the statistical tests.

Results

Of the 156 species examined, 96 (61.5%) were assessed to be described species and 60 (38.5%) to be undescribed (Table 1).
This sub-sample represents 10.6% of the beetle species collected (Stork & Grimbacher, 2006). For species, the canopy-to-ground ratio in the sample (1.4:1) was not significantly greater than for the remainder (1.2:1). (ANOVA $F_{1,8} = 2.68, P = 0.14$). For individuals, the canopy-to-ground ratio for the analysed species (1.9:1) was only marginally significantly greater than for the remainder (0.8:1) (ANOVA $F_{1,8} = 4.85, P = 0.059$). Although the mean abundance of described species (mean = 44.0, SE = 3.0) was higher than for undescribed species (mean = 29.4, SE = 2.7), these differences were not statistically significant (ANOVA $F_{1,8} = 0.25, P = 0.63$). ‘New’ undescribed and described species were found in each of the 4 years of sampling. There were no significant differences in the number of described (ANOVA $F_{3,16} = 0.74, P = 0.54$) or undescribed (ANOVA $F_{3,16} = 0.68, P = 0.58$) species caught in each of the four separate years of sampling.

Significantly, more described species were captured in the canopy than near the ground (ANOVA $F_{1,8} = 13.30, P = 0.007$, Fig. 1). Although there were slightly more undescribed species caught in canopy traps than in ground traps (Fig. 1), these differences were not statistically significant (ANOVA $F_{1,8} = 1.40, P = 0.27$). The mean body size of described species was significantly greater than that of the remainder and the undescribed species (ANOVA $F_{2,24} = 226.82, P < 0.001$; Fig. 2). Canopy species were also marginally larger than ground species (ANOVA $F_{2,24} = 4.03, P = 0.056$; Fig. 2), but there was no interaction between the two factors ($F_{2,24} = 1.11, P = 0.35$). For the described species, there was a significantly negative relationship between body size and year of description ($r^2 = 0.14, P < 0.001, n = 96$, $\log y = 5.618 - 0.003x$; Fig. 4).

Table 1. Numbers of individuals and species of beetles from an Australian lowland tropical rainforest. Left hand columns represent the total assemblage and right hand columns represent the subsample sorted into described and undescribed species.

| Family         | Total number of: | | Number of studied: | |
|----------------|------------------|------------------|
|                | Individuals      | Species          | Individuals | Described species | Undescribed species |
| Brentidae      | 65               | 12               | 62          | 8                  | 2                  |
| Carabidae      | 113              | 26               | 19          | 6                  | 0                  |
| Chrysomelidae  | 2547             | 70               | 1889        | 13                 | 8                  |
| Ciidae         | 67               | 8                | 63          | 0                  | 7                  |
| Cleridae       | 219              | 14               | 135         | 3                  | 1                  |
| Coccinellidae  | 294              | 35               | 71          | 7                  | 5                  |
| Curculionidae  | 2908             | 239              | 1324        | 24                 | 13                 |
| Dermestidae    | 325              | 8                | 16          | 0                  | 2                  |
| Discolomatidae | 5                | 2                | 4           | 0                  | 1                  |
| Dryophthoridae | 10               | 2                | 10          | 2                  | 0                  |
| Endomychidae   | 104              | 10               | 72          | 3                  | 0                  |
| Erotylidae     | 106              | 10               | 105         | 6                  | 3                  |
| Histeridae     | 510              | 12               | 7           | 3                  | 0                  |
| Laemophloeidae | 60               | 18               | 2           | 1                  | 0                  |
| Latridiidae    | 346              | 6                | 47          | 0                  | 2                  |
| Platodactylidae| 38               | 3                | 37          | 0                  | 2                  |
| Salpingidae    | 20               | 8                | 17          | 3                  | 3                  |
| Scarabaeidae   | 1177             | 36               | 742         | 13                 | 2                  |
| Scaptiidae     | 193              | 6                | 192         | 0                  | 5                  |
| Silvanidae     | 32               | 5                | 32          | 1                  | 4                  |
| Tenebrionidae  | 103              | 39               | 6           | 3                  | 0                  |
| Total          | 9242             | 569              | 4852        | 96                 | 60                 |

Fig. 1. Mean number (and SE) of described and undescribed species of selected families of beetles found in five canopy (open bars) and five ground (dark bars) malaise/flight intercept traps over 4 years in lowland rainforest at Cape Tribulation, Australia. **For canopy-ground test $P < 0.01$ (ANOVA).
Discussion

Factors influencing the proportions of undescribed species in rainforest strata

We have shown that there are significantly more described species in the canopy than the ground. Since our sub-sample was not significantly biased towards the canopy, and because there was no significant difference in the numbers of new species for the two strata, we must conclude that the number of new species does not appear to differ between the canopy and ground strata and that both strata represent important ‘biological frontiers’. This supports the earlier finding of Stork and Grimbacher (2006) that stratum-specific species are equally shared between the canopy and ground. In this respect, we feel that ground-based habitats have probably not received the attention they deserve.

If undescribed species are rarer, we would expect these to be less abundant than described species. However, for our data, this does not appear to be the case. This might be because a species that is less abundant in our sample might be common elsewhere in time and space. With respect to the latter explanation, we were not surprised to see additional species of both described and undescribed categories continuing to be sampled even in the fourth year. It was Wolda (1992), examining a 14-year data set from a continuous tropical insect sampling programme, who observed that tropical forest insect assemblages change over time, even in forest not subjected to any major disturbances. We should therefore expect additional species to continue to appear for many years.

Our results, showing that undescribed species are smaller than described species, confirm the findings of a number of other studies on insects (Gaston, 1991; Gaston et al., 1995), and other groups (Blackburn & Gaston, 1995; Reed & Boback, 2002; Diniz-Filho et al., 2005). The exceptions to this rule are studies of Australian and European scarabs (Allsopp, 1997; Cabrero-Sañudo & Lobo, 2003), where body size does not appear to be important in explaining year of description. We suggest that for these beetles, the methods of collecting are probably not body-size selective and therefore whether a species is described is not body-size dependent. It is clear from a range of other studies that the factors determining whether a species is described or not are complex. For example, studies of the species of Western Palaearctic Aphthona (Coleoptera: Chrysomelidae; Baselga et al., 2007) have shown that, although pure effects of geographical range size, trophic variables and geographical location of taxa are negligible, shared effects of these explain 64% of the variance such that widely distributed and trophic generalist species in northern western parts were described first. In this respect, the geographical distribution of taxonomists and collecting effort are well-known factors in determining whether species are described or not (Patterson, 1994; Stork, 1994).

As expected we found a higher proportion of herbivore and xylophage species to be described than those of other feeding groups, because beetles with these feeding ecologies are significantly larger than predators, fungivores and saprophages (Grimbacher & Stork, 2007) and larger species are more likely to be described (this study). Some authors have suggested that non-phytophagous insects have received less attention than phytophagous insects (Kitching, 2006; Stork, 2007b), and we hypothesise that it is in these groups that most new species will be found.
Difficulties in determining new species

A sample of 156 beetle species might be considered small, but this belies the high level of investigation required to determine whether a species is new or not. We believe this to be the reason why others have not taken our approach to looking at what kinds of species are likely to be undescribed. A full revision of a taxon with 156 species could amount to several years of effort for a taxonomist. Most tropical-insect ecologists looking at insect communities sort species to morphospecies or ‘recognisable taxonomic units’, because full identification can require complex dissections, measurements and comparison with type specimens that may be located in many museums across the world. This difficulty is further compounded by the fact that some groups have not been studied since pioneering work by taxonomists in the 1800s and are considered taxonomically highly intractable. We therefore recognise that there is a taxonomic bias in our selection of families in favour of those for which there currently are specialist taxonomists, and we suspect that the proportion of undescribed species may be higher than 38.5% for the groups we examined.

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References


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