

Which leaf beetles have not yet been described? Determinants of the description of Western Palearctic *Aphthona* species (Coleoptera: Chrysomelidae)

ANDRÉS BASELGA^{1,*}, JOAQUÍN HORTAL^{1,2}, ALBERTO
JIMÉNEZ-VALVERDE¹, JOSÉ F. GÓMEZ¹ and JORGE M. LOBO¹

¹Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales – CSIC, c/José Gutiérrez Abascal, 2, 28006 Madrid, Spain; ²Dpto. de Ciências Agrárias, Universidade dos Açores, Campus de Angra, Terra-Chã 9701-851, Angra do Heroísmo, Terceira (Azores), Portugal; *Author for correspondence (e-mail: baselga@mncn.csic.es)

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Abstract. The degree of completeness of the western Palearctic inventory of the genus *Aphthona* and the factors that have determined the process of species description in the region were analysed. The historic species accumulation curve shows no asymptotic trend so no accurate estimations could be made of the number of species to be discovered in the future, but the shape of the curve indicates that a significant proportion of the taxa remains yet-to-be-described and thus further taxonomic effort will be needed. In order to optimise this taxonomic work, several morphologic, trophic and geographic variables of *Aphthona* species were analysed, in a search for the factors that have influenced the probability of discovery of taxa and thus to estimate the characteristics of the yet-to-be-described species. General Regression Models and variation partitioning were used to assess the influence on the process of species description of body size and colour, trophic range, number of host plants, geographic range size, maximum and minimum latitude and longitude. Morphological variables are not statistically significant in explaining the variation in the year of description, whereas trophic and geographic variables are essential determinants. The pure effects of geographic range size, trophic variables and geographic location of taxa are negligible, but the shared effects between the three groups of variables account for important portions of the variation; the whole model explains 64% of the variance. Widely distributed and trophic generalist species living in northern and western areas of the western Palearctic region were described first. Extrapolation of the observed pattern should yield an estimate of the probable features and location of the yet-to-be-described species. New *Aphthona* should be searched for southwards and eastwards, distributed in small areas and living on a single, or very few, host plants.

Introduction

Taxonomy should play a crucial role in combating the biodiversity crisis. Current approaches to Conservation Biogeography need to overcome the effects of the lack of taxonomic knowledge, among others (Whittaker et al. 2005): the so-called Linnaean shortfall, i.e. the great amount of the diversity expected to exist but yet to be described and catalogued (Brown and Lomolino

1998). Though several opinions have been expressed and different solutions to such a shortfall proposed, all agree that taxonomy is a 'good science' with intrinsic value that should not be continuously asked to justify its role in biodiversity conservation (de Carvalho et al. 2005). The process of describing new species is the first step in taxonomic science, and thus the basis for any biodiversity-related research. However, inventories are still far from complete because a large proportion of invertebrates remains to be discovered (May 1988; Erwin 1991; Gaston 1991a; Godfray et al. 1999; Odegaard 2000; Odegaard et al. 2000).

The influence on the process of species description of variables such as body size, geographical range size and geographical location of taxa has been explored for several heterogeneous groups (Gaston and Blackburn 1994; Blackburn and Gaston 1995; Gaston et al. 1995a; Allsopp 1997; Cabrero-Sañudo and Lobo 2003; De Grave 2003; Collen et al. 2004; Gibbons et al. 2005). On the other hand, the degree of completeness of faunistic inventories and the amount of descriptive work yet to be done can be estimated by examining the historic growth of the cumulative number of taxa (Medellín and Soberón 1999; Cabrero-Sañudo and Lobo 2003; Baselga and Novoa 2006). The combined knowledge of the proportion of species that remains undescribed and of factors that determine the description process should be very useful to the design of efficient strategies of taxonomic research and optimisation of future efforts.

In this paper we analyse how the species of a large genus of Chrysomelidae, *Aphthona* Chevrolat, have been described in the western Palaearctic region and the factors that have influenced this process. This genus has around 500 recognised species distributed in the Palaearctic, Oriental, Australian and Afrotropical regions (Konstantinov 1998). Two modern revisions have been devoted to Palaearctic *Aphthona* (Heikertinger 1944; Konstantinov 1998) so it could be considered a well known group from the taxonomic point of view, when compared with other genera. However, new papers are continuously adding new taxa to the *Aphthona* inventory (Fritzlar 2001; Konstantinov et al. 2001; Baselga and Novoa 2002; Fritzlar 2004) and no estimation of the total number of species living in the western Palaearctic region is available. Therefore, the aims of this paper are: (i) to analyse the degree of completeness of the western Palaearctic inventory of *Aphthona*, (ii) assess the relative importance of several geographic, trophic and morphologic characteristics of *Aphthona* species in determining the probability of discovery and thus the historic pattern of description, and (iii) use such knowledge to estimate the probable characteristics and location of the yet-to-be described taxa.

Materials and methods

Taking into account current taxonomic knowledge (Konstantinov 1998) together with posterior contributions (Fritzlar 2001; Konstantinov et al. 2001;

Doguet and Bergeal 2001; Baselga and Novoa 2002; Fritzlar 2004), a total of 82 *Aphthona* species were described or recorded from the western Palaearctic region through 2004. This area includes Europe to the Ural Mountains, Caucasus, Anatolian peninsula, Iran, Middle East, North Africa and Macaronesia (Vigna Taglianti et al. 1992). To estimate the actual number of *Aphthona* species in the region and thus the number of taxa to be discovered in the future, we used the cumulative number of species described in the studied area from 1777 [description of the first western Palaearctic species: *Aphthona nonstriata* (Goeze)] to 2004, fitting an asymptotic function to the historic curve (Medellín and Soberón 1999; Cabrero-Sañudo and Lobo 2003; Baselga and Novoa 2006). The logarithm of the cumulative number of described species was plotted against the year (Cabrero-Sañudo and Lobo 2003) and the asymptotic Clench function was fitted to the curve by non-linear regression (Simplex and Quasi Newton algorithm; StatSoft 2001).

In order to model the year of description we have explored nine explanatory variables: body size and colour, trophic range, number of host plants, geographic range size, maximum and minimum latitude and longitude. The effect of several of these factors as determinants of the description date was previously explored for other groups (Gaston and Blackburn 1994; Blackburn and Gaston 1995; Gaston et al. 1995a; Allsopp 1997; Cabrero-Sañudo and Lobo 2003; De Grave 2003; Collen et al. 2004; Gibbons et al. 2005). Body colour, a surrogate of conspicuousness, was scored in three classes according to its showiness (1: light brown, 2: dark brown to black, 3: metallic coloured). Trophic range was categorised in three classes (1: monophagous, 2: oligophagous, 3: polyphagous) following Biondi's definitions (Biondi 1996). Both variables are treated as dummy, together with body size and number of host plants, extracted from Konstantinov (1998) and previous monographs (Heikertinger 1944; Doguet 1994), or the original descriptions for species described later (Fritzlar 2001; Konstantinov et al. 2001; Baselga and Novoa 2002; Fritzlar 2004). Values of maximum and minimum latitude and longitude were estimated using the available distribution data (Gruev and Döberl 1997; Konstantinov 1998) or the original descriptions for species described later. Finally, geographic range size was estimated computing the area comprised in the rectangle delimited by maximum and minimum latitude and longitude.

Multiple relationships between the year of description and the explanatory variables were analysed using general regression models (GRM) (StatSoft 2001). Continuous variables were standardised to 0 means and 1 standard deviation to avoid scale effects. Categorical variables, and the linear, quadratic and cubic functions of the continuous predictors were independently regressed against the response variable, to determine significant relationships. Significant terms were selected by means of a backward stepwise procedure. Finally, variation partitioning among significant explanatory variables was used to quantify the relative importance of the pure effects of each determinant, and its respective shared influences (Legendre and Legendre 1998). After rejecting those variables only slightly, or not at all, related with the date of description,

total variation in the date of description was decomposed among three groups of variables: TS = trophic selection variables (trophic range and number of host plants), GRS = geographic range size and GL = geographic location variables (latitudinal and longitudinal), and the percentage of explained deviance calculated for eight different components (Figure 1a): *a* = pure effect of GRS alone, *b* = pure effect of TS alone, *c* = pure effect of GL alone, *d* = combined variation due to the joint effect of GRS and TS components, *e* = combined variation due to the joint effect of GRS and GL components, *f* = combined variation due to the joint effect of TS and GL components, *g* = combined variation due to the joint effect of the three components, and variation not explained by the independent variables included in the analysis (*U*). The decomposition of the variation in the description year into the three sets of explanatory variables was carried out by means of a partial regression analysis (Legendre and Legendre 1998). Such an approach allows non-independent explanatory variables to be dealt with, as it is explicitly designed to identify the portions of explained variability that are shared by different factors, and those that are independent (Cabrero-Sañudo and Lobo 2003; Heikkinen et al. 2004; Lobo et al. 2004). In the process of variation decomposition, the date of species description (*y*) was regressed with the three types of variables together (GRS, TS and GL), which represent the total explained variation in the data set ($a + b + c + d + e + f + g$ in Figure 1). Regressing *y* with each one of the explanatory variables yields the variation separately attributable to GRS ($a + d + e + g$), TS ($b + d + f + g$), and GL ($c + e + f + g$). Subsequently, residuals of the regression of GRS against TS + GL variables were calculated, and *y* was regressed with these residuals in order to estimate the pure effect of GRS variation (*a*). Fractions *b* and *c* were estimated in the same way after computing the regression residuals of TS against GRS + GL, and the regression residuals of GL against TS + GRS, respectively. The remaining variation fractions were computed according to two sets of equations (Borcard et al. 1992), where:

$$d + e + g = \text{GRS} - a$$

$$d + f + g = \text{TS} - b$$

$$e + f + g = \text{GL} - c$$

and

$$d = (\text{GRS} + \text{TS}) - (e + f + g) - (a + b)$$

$$e = (\text{GRS} + \text{GL}) - (d + f + g) - (a + c)$$

$$f = (\text{TS} + \text{GL}) - (d + e + g) - (b + c)$$

$$g = (d + e + g) - d - e = (d + f + g) - d - f = (e + f + g) - e - f$$

Results

The first *Aphthona* species from the western Palaearctic region was described in 1777 and a total of 82 species were discovered through 2004 (synonyms excluded), with a rate of description of 0.36 species per year ($SD = 0.89$). This rate was quite homogeneous up to 1975 (Figure 2). However, one striking feature of this historic curve is the increase of description rate in more recent years, up to 0.67 species per year ($\pm 1.11SD$) from 1990 to 2004. The shape of the curve shows that the inventory of western Palaearctic *Aphthona* is far from complete, with no asymptote yet approached, so no accurate estimations could be made of the number of species to be discovered in the future. Tentatively, in order to make possible the fitting of the Clench function to this curve, a logarithmic scale was used, with the computed asymptotic value taken to be 492 species (six times the present number). This extremely high value cannot be considered a realistic estimate of the true species richness of *Aphthona* in the region, but points to the fact that a significant proportion of the taxa remain undescribed.

With exception of body size, colour and minimum latitude, all the following variables turn out to be statistically significant when regressed against the description year (Table 1, Figure 3). The wider the trophic range, and the greater the number of host plants, the earlier the species description. In the same way, the

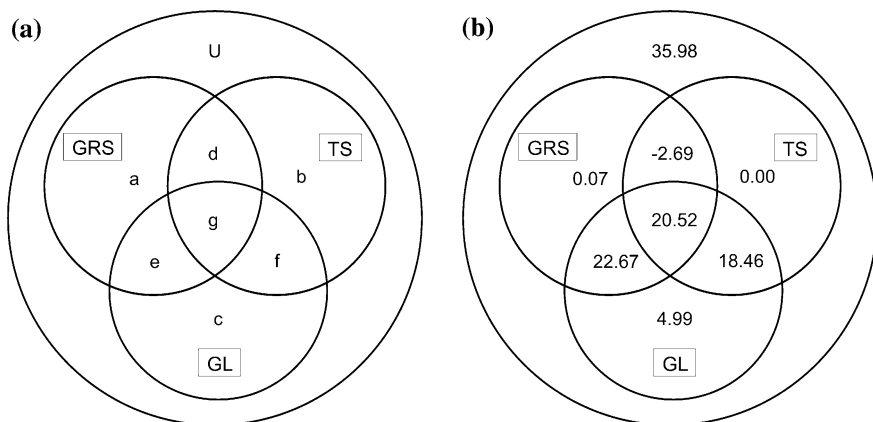


Figure 1. (a) Diagram showing the variation in the dependent variable (year of description) due to three groups of explanatory variables, GRS = geographic range size, TS = trophic selection, GL = geographic location: U is the unexplained variation; a, b and c are the pure effects of GRS, TS, and GL, respectively; d, e and f are the combined variation due to the joint effect of GRS and TS, the joint effect of GRS and GL, and the joint effect of TS and GL, respectively; g is the combined variation due to the joint effect of the three variables. (b) Variation partitioning in the year of description of *Aphthona* species between the three groups of explanatory variables selected. The decomposition of the variation has been carried out by partial regression analysis (Legendre and Legendre 1998) using General Regression Models.

wider the geographic range size, and the higher the maximum latitude and longitude, the earlier the species description. Minimum longitude shows an inverse relationship. Backward stepwise processing of these six variables yielded a model with quadratic function of number of host plants and linear functions of maximum and minimum longitude as significant variables. Trophic range, maximum latitude and geographic range size were removed from the model, which explains 63.95% of variance ($F_{(4, 62)} = 27.50, p < 0.001$). Considering each group of explanatory variables, the model for TS only retains the quadratic function of the number of host plants ($F_{(2, 64)} = 18.05, p < 0.001, R^2 = 34.04\%$), whereas trophic range is removed. The complete model for GL is comprised of the quadratic function of maximum longitude and linear functions of maximum latitude and minimum longitude ($F_{(4, 62)} = 25.30, p < 0.001, R^2 = 62.00\%$). The GRS model is composed of a single variable whose quadratic function is statistically significant ($F_{(2,79)} = 26.96, p < 0.001, R^2 = 40.56\%$).

The variance partitioning among all the significant explanatory variables shows that pure effects of TS and GRS provide a negligible portion of explanation (0.00 and 0.07%, respectively) (Figure 1b). The pure effect of GL accounts for 5% of the variation in the date of description. Important portions of the variation are explained by shared effects of pairwise combinations of variables. The combined effect of TS-GRS produces a negative value (−3%), pointing to possible synergy between the two variables (Legendre and Legendre 1998). The shared effects of GRS-GL and TS-GL are much greater (23 and

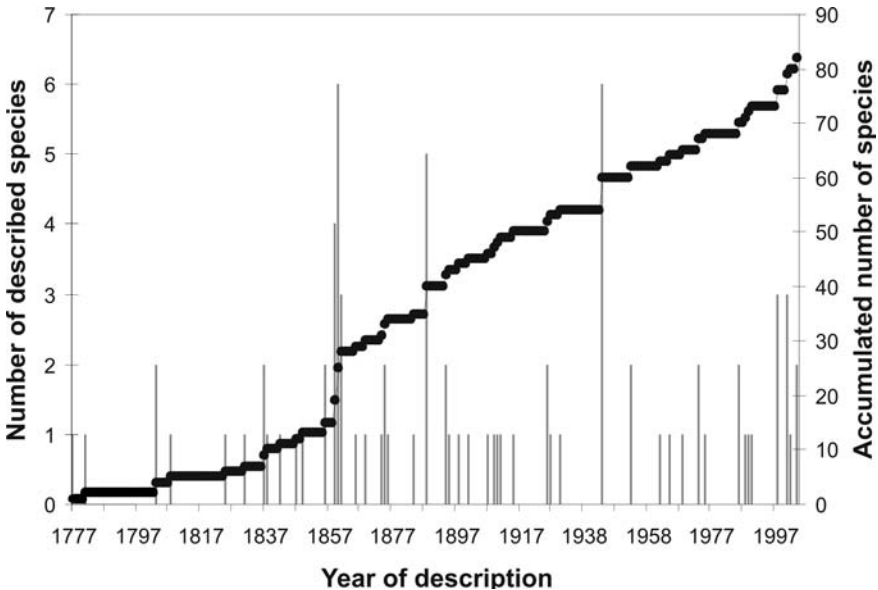


Figure 2. Number of described *Aphthona* (bars) and temporal variation from 1777 to 2004 in the cumulative number of species living in the Western Palaearctic region (dots).

Table 1. Explored variables related to the description year and models for each group of variables, respective regression coefficients and percentage of explained variance (R^2). f^2 is the quadratic function of the variable considered.

Variable	Function	R^2 (%)	F	p
Geographic range size	Quadratic	40.56	26.96	<0.001
Trophic range	–	37.87	15.85	<0.001
Number of host plants	Quadratic	34.04	20.38	<0.001
Maximum latitude (y max)	Quadratic	40.67	27.07	<0.001
Minimum longitude (x min)	Linear	28.61	32.06	<0.001
Maximum longitude (x max)	Linear	6.84	5.87	0.018
Minimum latitude (y min)	Linear	1.58	1.28	ns
Body colour	–	1.20	0.48	ns
Body size	Linear	0.21	1.17	ns
Model for GRS	f^2 geographic range size	40.56	26.96	<0.001
Model for TS	f^2 number of host plants	34.04	20.38	<0.001
Model for GL	y max + f^2 x max + x min	62.00	25.30	<0.001
Whole model for GRS + TS + GL	f^2 n hosts + x max + x min	63.95	27.50	<0.001

18%, respectively). Finally, 20% of the variance in the date of description is indistinguishable, being explained by the collinear effect of the three groups of variables, while around 35% of the variation cannot be attributed to any of the variables considered.

Discussion

The historic curve of the cumulative number of species described from the western Palaearctic region clearly indicates that the current state of the inventory is far from complete. The increase of the rate of species description in recent could be attributed to the stimulating effect of the appearance of a taxonomic revision (Konstantinov 1998) that facilitates the recognition of new taxa. The description rate should decline in the future, but both the shape of the curve previous to the revision and the subsequent increment in the taxonomic activity indicate that a number of taxa will be discovered in the future before the curve's asymptote is approached. The lack of asymptotic trend makes any accurate estimate of the actual number of *Aphthona* species living in the area studied unfeasible. Even adjusting an asymptotic function to the curve using a logarithmic scale (Cabrero-Sañudo and Lobo 2003), fails to yield a realistic estimate. The logarithmic scale makes fitting of the function possible but any small variation in the data or in the selected asymptotic function (Flather 1996) may yield highly different estimates (not shown). Therefore, taking into account the small percentage of known taxa estimated by this model we can expect that any future addition of new data will greatly alter estimates. For the moment, the only pertinent conclusion is that a significant percentage of taxa remains undescribed and thus an important further

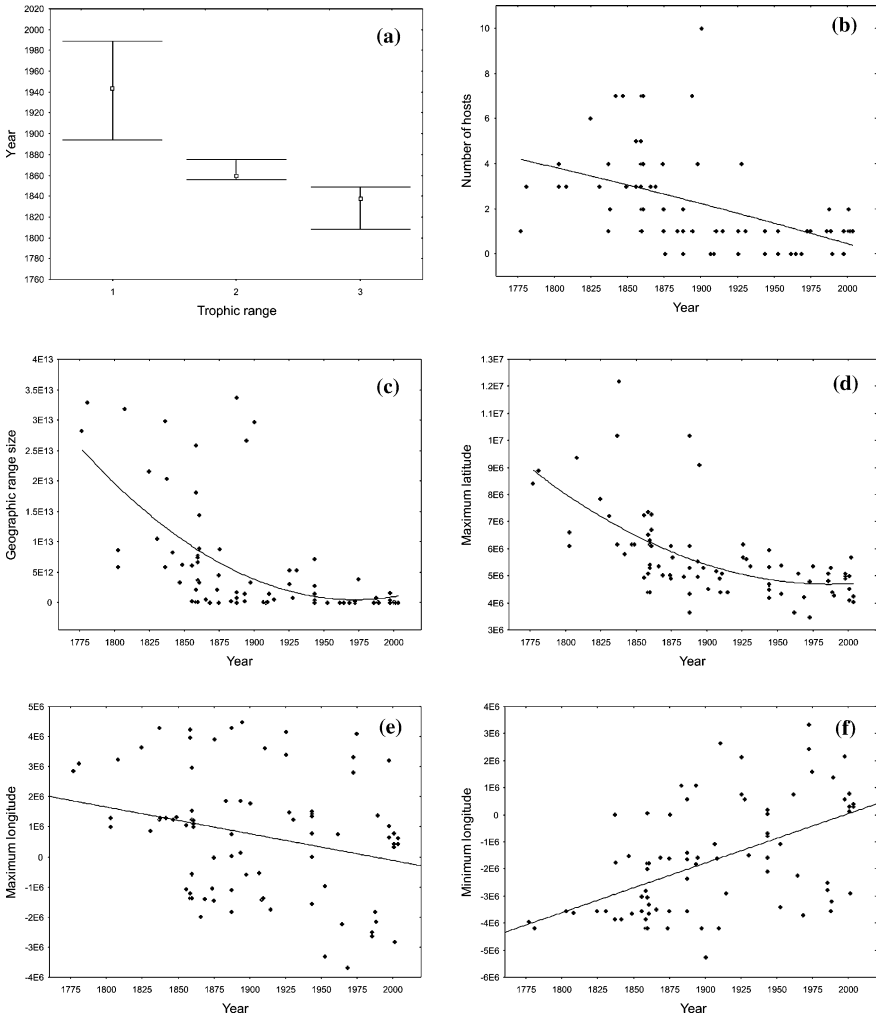


Figure 3. Relationship between the date of species description and the statistically significant variables related to the year of description of *Aphthona* species (Table 1): (a) Trophic range (median and 25–75% percentiles). (b) Number of host plants. (c) Geographic range size. (d) Maximum latitude. (e) Maximum longitude. (f) Minimum longitude.

taxonomic effort is still needed, even for the presumably ‘well-known’ western Palearctic region and genus *Aphthona*.

This future descriptive effort should be optimised by extrapolating the trends observed in the historic process of species discovery. This pattern is determined by many factors, some of them unknown, but our assessment of the influence of body size and colour, trophic range, geographic range size and geographic location allows us to make several estimations of the probable characteristics

of the yet to-be-described taxa. The variables considered account for 64% of total variation in the year of species description, and the residuals of the whole multiple regression model are not spatially autocorrelated (highest value of Moran's $I = 0.165$) (Gamma Design 2001), showing that though several other unaccounted-for factors might influence the description process, it seems that no spatially structured variables are lacking in our analysis (Diniz-Filho et al. 2003; Hawkins and Porter 2003).

The detectability of species influences its probability of description in some groups. Body size is responsible for an important amount of explanation for British beetles (Gaston 1991b) or North American butterflies (Gaston et al. 1995a), but responsible for a negligible proportion of variation for Australian and western Palaearctic dung beetles (Allsopp 1997; Cabrero-Sañudo and Lobo 2003). In the case of western Palaearctic *Aphthona*, it seems that neither size nor colour differences influence the rate of species description. The small size of all the species on a human scale make differences ranging from 1.5 to 4.0 mm (and probably also between colours) irrelevant for the entomologist's eye. Another reason may be the unspecific sampling method usually employed to collect *Aphthona*, sweeping its herbaceous host plants that are thus difficult to isolate from contiguous vegetation, so samplings catch beetles independently of conspicuousness.

On the contrary, species range size, the degree of trophic specialisation and the geographical location of taxa are essential variables related to the *Aphthona* description process, especially the latter; considering also the shared effects with other variables GL explains 62% of the variance. The importance of geographical location as a factor explaining the probability of description was previously established for several groups (Gaston et al. 1995b; Allsopp 1997; Cabrero-Sañudo and Lobo 2003). In the case of *Aphthona* the importance of these variables are due to a negative correlation between description date and maximum latitude and longitude, and a positive correlation between description date and minimum longitude that these species can attain. Therefore, species with distributions reaching the northern and western limits of the Palaearctic region were described first, as was the case with dung beetles (Cabrero-Sañudo and Lobo 2003). Geographic range size is also a general determinant of the year of description (Gaston et al. 1995a; Allsopp 1997; Cabrero-Sañudo and Lobo 2003; Collen et al. 2004; Gibbons et al. 2005). In the case of western Palaearctic *Aphthona* there is a negative curvilinear relationship between description year and GRS that accounts for 40% of total variance, but its effect is inextricably joined to the other two variables. The effect of TS is explored in this paper for the first time; our results show that it is an important factor for this group of phytophagous beetles, explaining 38% of the total variation. Both variables included in TS, trophic range and number of host plants, are negatively correlated with description date, so generalist species seem to have been described at an earlier date than specialised ones. The pure effect of TS is negligible, but the joint effect of TS and GL is very important. We suspect that the reason for this shared effect is the correlation

found between trophic range and maximum latitude (Kruskal–Wallis anova non-parametric test = 11.96, $p = 0.003$), and between number of host plants and maximum latitude (Spearman Rank non-parametric correlation test = 0.42; $p < 0.05$).

The rationale for the strong influence of all these variables in the discovery of new species is the combination of the historic distribution of taxonomists and geographically structured biological gradients. On the one hand, taxonomists were first established in northern and western countries; the 10 first species, for example, were described by Goeze (Germany), Schrank (Austria, Germany), Koch (Germany), Gyllenhal (Sweden), Duftschmid (Austria), Stephens (England), Faldermann (Germany, Russia), Curtis (England) and Zetterstedt (Sweden), and taking into account the oversampling produced in areas close to recorders' bases (Dennis and Thomas 2000), species living in northern and western European countries tended to be described first. On the other hand, northern zoological assemblages are mainly constituted by postglacial colonizers (Taberlet et al. 1998; Hewitt 1999; Schmitt et al. 2003; Schmitt and Krauss 2004; Sommer and Benecke 2004, 2005) which seem to have managed to settle in new habitats. In most cases, these northern species tend to have a wide trophic range (making possible the use of new resources) and also broader distributions than southern ones because the latter have not abandoned their old restricted ranges, and thus their distributions are smaller. In summary, the earlier appearance of northern European taxonomists have produced that taxa with large distributions and wide trophic range living in northern Europe were described first.

The accumulation of information with the passing of time could bias present results; the earlier the species description, the more information available on its trophic and geographic range. From this point of view, causality should be reversed because the relations between variables and description date would reflect the time available for the accumulation of data by taxonomists, not the probability of discovery of each species. This effect would be negligible if current descriptions and taxonomic reviews were exhaustive, making distributions and trophic data almost as complete for recent taxa as for older ones. To assess such possible bias we limited the regression to the species described before 1975 (68 taxa), considering 30 years of taxonomic work (given the present distribution of taxonomists and sampling effort) enough to accumulate trophic and geographic information, making differences with older species insignificant. Therefore, if the amount of variation explained by variables in the period previous to 1975 were lower, we should conclude that trends are the result of the accumulation of information and not a pattern produced by the probability of discovery. Excluding species described after 1975, all the explored variables explain similar percentages of total variance to those obtained considering the complete inventory (trophic range: 33%, quadratic function of number of hosts: 29%, quadratic function of maximum latitude: 35%, minimum longitude: 36%). The only exception is the geographic range size, which explains only 21% of total variation before 1975. Therefore, we conclude that the narrow trophic ranges and southern

and eastern locations of newly described taxa are actual characteristics and not artefacts due to the lack of information, but that small geographic range sizes of recent taxa are biased by lack of information, and thus the geographic range size relationship with the year of description is due both to the higher probability of description of wide range species and to the accumulation of new records with the passing of time.

Finally, extrapolation of the observed pattern should yield an estimate of the probable features and location of yet-to-be-described species, aiding entomologists to optimise research efforts. In the western Palaearctic region new *Aphthona* should be searched for southwards and eastwards, distributed in small areas and living on a single or very few host plants. Therefore, we should select small geographically or ecologically isolated areas (i. e. mountain areas, relict woodlands) in southeastern Europe, northeastern Africa, Turkey, Caucasus, Iran and prospect plants not previously explored and with restricted distributions too. Probably this taxonomic and geographic bias is common to most invertebrate groups, which represent the greatest proportion of biological diversity. Taxonomic effort should therefore be explicitly focused on such poorly-known taxa and regions.

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