

Predicting Total Global Species Richness Using Rates of Species Description and Estimates of Taxonomic Effort

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Abstract.—We found that trends in the rate of description of 580,000 marine and terrestrial species, in the taxonomically authoritative World Register of Marine Species and Catalogue of Life databases, were similar until the 1950s. Since then, the relative number of marine to terrestrial species described per year has increased, reflecting the less explored nature of the oceans. From the mid-19th century, the cumulative number of species described has been linear, with the highest number of species described in the decade of 1900, and fewer species described and fewer authors active during the World Wars. There were more authors describing species since the 1960s, indicating greater taxonomic effort. There were fewer species described per author since the 1920s, suggesting it has become more difficult to discover new species. There was no evidence of any change in individual effort by taxonomists. Using a nonhomogeneous renewal process model we predicted that 24–31% to 21–29% more marine and terrestrial species remain to be discovered, respectively. We discuss why we consider that marine species comprise only 16% of all species on Earth although the oceans contain a greater phylogenetic diversity than occurs on land. We predict that there may be 1.8–2.0 million species on Earth, of which about 0.3 million are marine, significantly less than some previous estimates. [Biodiversity; biogeography; deep-sea modeling; macroecology; marine; taxonomy; terrestrial.]

Speculation as to how many species exist on Earth has excited scientists for at least 260 years (Ødegaard 2000), and estimates vary by tens of millions. Even the number of described species is uncertain because an inventory that accounts for multiple descriptions of species is not yet available. However, Species 2000's Catalogue of Life (CoL) has inventoried over 1.2 million (Bisby et al. 2010) of the estimated 1.5 million described species (May 1998). We favour the 1.5 million estimate because evidence suggests that at least 20% of currently recognized species are likely to be found to be synonyms (e.g., Alroy 2002; Gaston and Mound 1993; Solow et al. 1995; May 1998, 2002, 2010) and only known synonyms are accounted for in other estimates (e.g., Chapman 2009). Methods of estimating species richness that involve scaling up from ratios of species in particular geographic areas and habitats are compromised because taxa do not always show consistent gradients in richness across environments, latitude, altitude, depth, or beta diversity (Gaston 1991; Bartlett et al. 1999; Novotny et al. 2006; Costello, Coll, et al. 2010), and the rate of discovery of species has varied between habitats and environments. Thus, with our present state of knowledge, predictions based on description rates may have a sounder theoretical and empirical basis than extrapolations using species ratios (Costello and Wilson 2011), and an improved method of predicting future discoveries has been developed (Wilson and Costello 2005). However, no statistically based methods to predict how many species may exist have been applied across all taxa and environments.

In this paper, we have predicted future discoveries using global species databases (GSD) totalling over 580,000 species from marine, terrestrial, and freshwater

environments, from their rates of description. Weaknesses of using species descriptions are their sensitivity to variation in rates of synonymy and to taxonomic effort (O'Brien and Wibmer 1979; Alroy 2002; Joppa et al. 2011). Synonym rates vary by taxa, but can be 7–80% in different insect orders and families (Gaston and Mound 1993; Gaston et al. 1995), were 81% in European freshwater fish (Kottelat 1997), between 58 and 78 % for seed plants (Scotland and Wortley 2003), and 37% for molluscs (Bouchet 1997). To minimize variation due to synonyms, the present study only used data that had accounted for known synonyms. We have not tried to account for as yet unrecognized synonyms, for synonyms that may later be found to be valid, or that some future “species” will be synonymized. Despite a large literature claiming that there has been a decline in taxonomic expertise, analyses of expertise are more equivocal (Costello, et al. 2006), and in general, the number of scientists and their publications has been increasing in recent decades (Frank and Curtis 1979; Alroy 2002; Zapata and Robertson 2007; Ware and Mabe 2009; Eschmeyer et al. 2010; Pimm et al. 2010). Joppa et al. (2011) fitted a nonlinear regression model to predict the total number of flowering plant species, with one of the regressor variables being the number of taxonomists' actively describing species in a 5-year period. Unfortunately, their model lacked an estimate of the uncertainty in their prediction. Bebber et al. (2007) correctly concluded that using description rates was problematic because of variable taxonomic effort and because lack of flattening out of the cumulative description rate curve. In this paper, we analyzed trends in authorships of species descriptions over time to see if there were indications of increased or decreased taxonomic effort that

may influence the rate of description, and we calculated confidence limits to quantify the variation in the rate of description. Therefore, this paper provides the most comprehensive and statistically rigorous approach to date that predicts global species richness while considering sampling effort.

METHODS

We analyzed data compiled from the World Register of Marine Species (WoRMS) version Aphia20091106.zip downloaded on 8 December 2009 (Appeltans et al. 2010) and the 2009 issue of the CoL (Table S1). Supplementary material is available at <http://www.sysbio.oxfordjournals.org> and includes details of methods, tables, figures, and citations of databases used in our analysis. The inclusion of marine taxa maximized coverage of all phyla and classes of life on Earth. Only CoL databases covering terrestrial species were used, although several taxa will include species that will have larvae and/or life stages living in freshwater environments. All have attempted to account for synonyms. However, the largest, LepIndex, based on the catalog of the butterflies and moths in the collections of the Natural History Museum (London) may include multiple names for the same species (Roskov Y., personal communication).

GSD in CoL that included significant numbers of marine species, and which lacked years of description for many species, were excluded from the analysis (Table S2). Apparent duplicated entries in GSD were filtered out. It is the practice in botany and some animal groups to also include the author and year of when a species was reclassified into a different genus. In these cases, the species were also omitted to avoid using the year of taxonomic revision rather than the first year of description. The years covered by the data went from 1758 to 2009, but we only included the years 1761–2000 in most graphs to exclude the large number of descriptions at the onset by Linnaeus, and the time lag in recent data publication and entry into the databases.

The number of distinct author surnames were extracted from each database. Different authors with the same surname were not distinguished, nor different names (e.g., spelling variants) for the same author; such occurrences were assumed to not significantly alter the trends in the number of authors reported per year. Except for the instance of Linnaeus (as Linne and L), manual correction of such occurrences was not practical due to the size of the databases analyzed. From the 1970s onward, there was an increasing use of the Latin et al. for indicating additional author names further to a given first author. Further details of the computational processes to identify distinct authors surnames, and account for multiple authors and use of “et al.” authors, are in the supplementary material.

To study the taxonomic effort more closely, we considered whether there had been a change in specialization effort by authors over time in three ways. First, we analyzed the duration of surnames in the data sets. To

prevent counting surnames from different authors, we only counted a surname for 30 or 40 years from its first occurrence. We assumed that the number of authors with the same surnames at the same time to be random over time and not affect the trend. Second, we looked at what proportion of species were described by the 10% most prolific authors each decade. This was calculated per decade, so if an author described many species in one decade and none in others then he or she would be counted as prolific only in that one decade. Finally, we calculated Pearson's skewness coefficient ($= 3 * (\text{mean} - \text{median}) / (\text{standard deviation})$) in the number of species described by authors over time.

A stochastic process model was fitted to the description data and the fitted model was then used to make predictions of numbers of species to be described by 2050, 2100, and in total. These models produced estimates of uncertainty in their predictions based on the observed variation in description rates from year to year. The model that was used is the nonhomogeneous renewal process (NHRP) of Wilson and Costello (2005) that has a trend and a variation component. For the trend, a logistic-type function was used, which has been found to be a good description of the shape of discovery curves in several studies (reviewed by Costello and Wilson 2011). For the variation component, the NHRP has the advantage that this is independent of the trend, allowing any size of variation about the logistic trend, so its estimates of prediction uncertainty are not as ad hoc as with other statistical approaches. For example, the nonhomogeneous Poisson process is a more commonly used stochastic process model (Solow and Smith 2005; Bebbler et al. 2007), but its variation is a fixed function of the trend (actually the square root of the mean). Indeed, it has been found to underestimate the amount of error by about 20% (Costello and Wilson 2011).

RESULTS

The cumulative number of species described was almost linear for all species from the middle of the 19th century until the present (Fig. 1a). The period of greatest discovery was in the first decade of the 20th century (Fig. 1b). Interruptions in this rate during the World Wars were scarcely noticeable on the cumulative graphs but were evident when plotted as number of species described per year (Fig. 1b). Following the World Wars, the number of species described increased, and continued to increase after the 1950s for marine, but not other species (Fig. 1b). The apparent decrease in the rate of marine species in recent years was considered an artifact of the time delay in entering recent descriptions into WoRMS.

The number of authors describing species increased over time with decreases during the World Wars (Figure S1a,b). The relative increase was greater for species in WoRMS than CoL. In part, this increase may be due to multiple authors describing a species because before the 1960s it was rare for a species to be authored by more than one person (Figure S1c,d). The trend in multiple

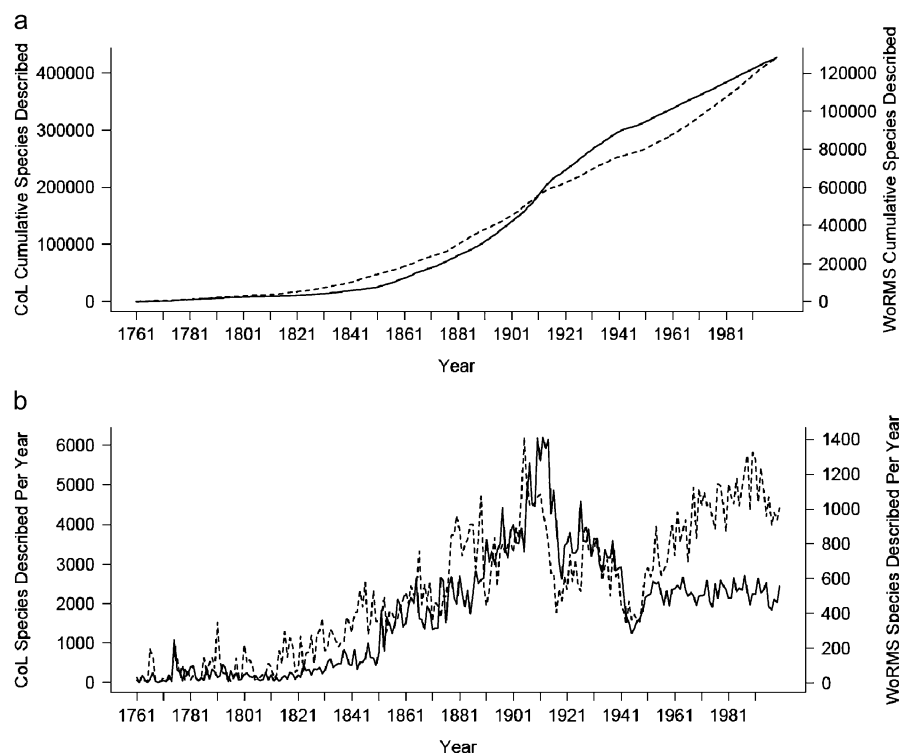


FIGURE 1. The number of species described each year in the WoRMS (dashed line) and CoL (solid line) databases as (upper panel) cumulative and (lower panel) actual number of species, up to the year 2000.

authorships was the same for the WoRMS and CoL data. The average number of authors per year accounted for this effect and still showed that more individuals were describing species since the 1960s (Fig. 2).

In contrast to the increasing number of authors over time, the number of species described per author has decreased since the 1920s, although less so for WoRMS than CoL (Fig. 3). The high variation in this ratio in the late 18th and early 19th centuries was due to relatively few species being described by few authors. Generally, there were more species described per author for the CoL than WoRMS data. The duration of author's publication years averaged 9.0 and 9.3 years for the WoRMS and CoL data, respectively (Figure S2) when publication lifetimes were limited to 30 years to avoid overestimates due to the same surnames reoccurring over time. When the recent decades were excluded because they constrain the potential lifetime, the average durations were 9.6 and 9.9 years, respectively. The average durations of surnames during the 10 decades from 1760 to 1860 and 1860–1960 were very similar, namely 9.7 and 9.5 for WoRMS, and 9.6 and 10.1 for CoL. The pattern over time was similar if a 40-year lifetime was used as the cutoff criterion although it resulted in longer average durations of 11.4 and 11.8 years. Over time, about 80% of CoL and 70% of WoRMS species were described by the most prolific authors (Figure S3). The proportion was more variable when there were few authors involved before the 1850s, and has been slightly lower in recent decades. The proportion of prolific authors measures

the “head” of the frequency distribution of species per author, whereas skewness measures its asymmetry. A skewness coefficient of <0.5 would indicate little to no skewness, and close to 1, high skewness. Because many authors described few species, and there were relatively few prolific authors, the skewness values were positive. This skewness was stronger for WoRMS (0.96) than CoL (0.66). That we noticed more variable skewness before the 1880s and less since then reflected the pattern in prolific authors. These measures of “specialization” of authors do not indicate any trend that might suggest more or less full-time taxonomists in recent decades.

Making predictions from earlier dates showed that the model underestimated the number of species later discovered (Fig. 4a). This would in part have been due to the effect of the decreased numbers of species described during the World Wars. In preliminary modeling we also observed that the best-fit model favoured an early leveling off. Thus, the model was conservative in underestimating rather than overestimating future discoveries. Furthermore, the model was also sensitive to when the peak rate of description occurred (Fig. 4b). To consider this effect, the forecasting of species richness was set to assume peak rates of discovery in 2010, 2050, and 2100 (Fig. 4b). If the peak period of discovery is now or in the future, then our predictions are significant underestimates (Fig. 4b). Considering that the number of species described per year in recent decades has not exceeded that in the early 20th century, this seems unlikely.

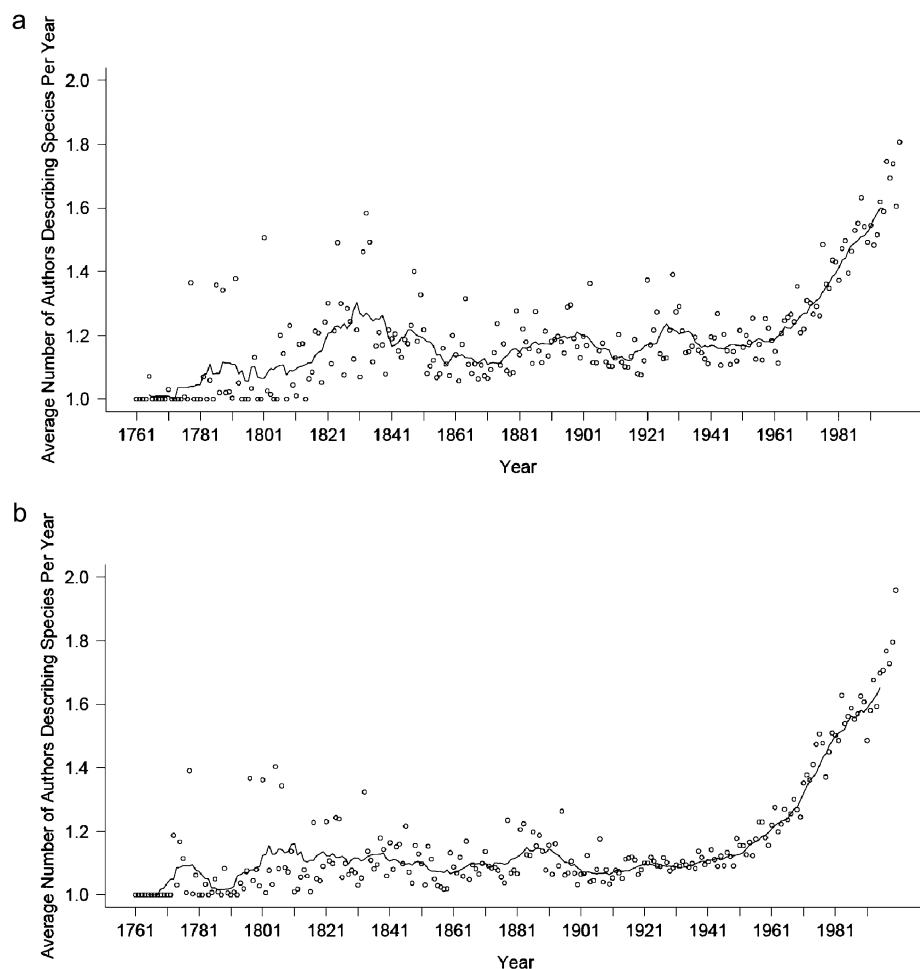


FIGURE 2. The average number of authors describing species each year in (upper panel) WoRMS and (lower panel) CoL global species databases. The dots represent actual values, and the solid line the 11-year moving average.

Several groups of marine and terrestrial species showed no sign of a slowing description rate by 2010, and so, although their mean and median predictions did not seem surprising, the confidence limits were wide (Tables 1 and 2). Thus, for several WoRMS and CoL databases, the estimates of the number of species in 2050 are reasonable, but less so for 2100, and they will be significant underestimates for the total remaining (Tables 1 and 2). The mean and median were similar in all cases, and the coefficient of variation was very low ($< 5\%$) for all databases except Echinodermata (Table 1). The proportion of species predicted to be discovered ranges from $< 1\%$ of the presently known marine birds and $< 7\%$ for mammals, to 124% for all fungi and 175% for marine isopod crustaceans.

The lower to upper predictions for the proportion of species yet to be described were 24–31% for marine and 21–29% for terrestrial species when modeled from 2009. The total number of species analyzed was 141,000 for marine and 370,000 for terrestrial. Thus, considering the upper and lower confidence limits on the predictions, we conservatively predict a further 40,000–56,000 ma-

rine and 79,000–108,000 terrestrial species are to be discovered from these taxa (Tables 1 and 2).

DISCUSSION

A problem in comparing predictions across taxa and geographic areas is the “ecologic fallacy” (Steel and Holt 1996), whereby data that are aggregated are analyzed and then the results are assumed falsely to extend to either the level of an individual or alternative aggregations. Such aggregations may be based on geography, or taxonomic groups, and were a weakness of previous approaches to extrapolate local data to global scales. Here we have minimized this effect by analyzing global species databases, as well as comparing across species rich taxa and environments. As the marine environment includes all but one of the phyla on Earth, it provides a unique perspective on biodiversity. Nevertheless, it must be recognized that our current knowledge of biodiversity is biased in several respects. Larger and more common species will be better known than the smaller and rarer, and relatively more marine species are known

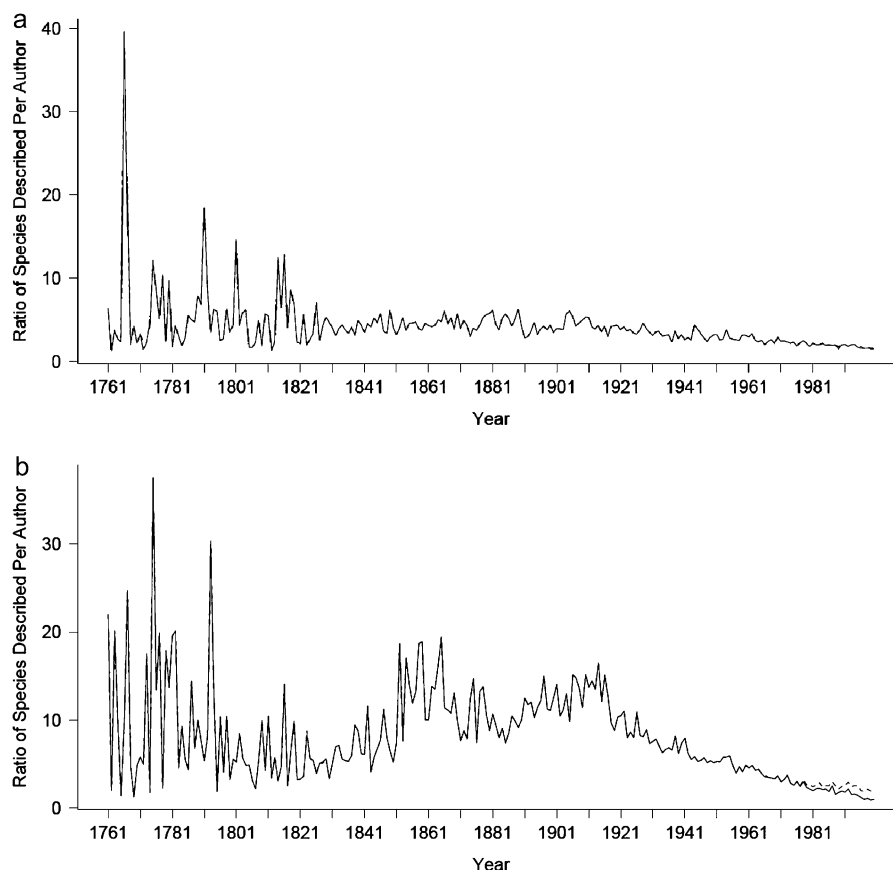


FIGURE 3. The ratio of species discovered to distinct author surnames for the (upper panel) WoRMS and (lower panel) CoL databases. The dashed line takes a minimum “et al.” effect into account, whereas the solid line is based on the empirical average to be consistent with Figure 2.

for the northern than southern hemisphere (Costello, Coll, et al. 2010).

We found the same patterns in both the marine and terrestrial data sets, namely:

1. the highest period of species descriptions was the first decade of the 20th century;
2. the increase in number of authors describing species over time;
3. the average publication life of an author being about 10 years;
4. the decline in number of species described and authors active during the World Wars;
5. the continued high rate of species discovery since the 1950s;
6. an increase in more than one author describing a species since the 1960s;
7. a decrease in the number of species described per author since the 1920s;
8. the range in the percentage of undiscovered species was similarly predicted to be between 24–31% and 21–29% of currently described species.

The key differences between the trends for the marine (WoRMS) and terrestrial (CoL) species were that for marine species:

1. there were generally fewer species described per author throughout time;
2. the rate of species description was higher since the 1950s;
3. the number of species described per year has increased since the 1950s;
4. the relative number of authors describing species was greater since the 1950s;
5. the decrease in number of species described per author per year since the 1920s has been subtle.

We attribute the higher rate of discovery, despite relatively fewer authors, for marine than terrestrial species to reflect the less explored nature of the marine environment. In other words, it has been easier to discover new species in the oceans than on land. It is thus fitting that exactly a century after the decade with the highest number of species described, the Census of Marine Life research programme has increased awareness in science and society of the opportunities to discover more about marine species (Costello, Coll, et al. 2010).

Taxonomic Effort

The increased number of authors per described species in recent years may reflect a change in practice whereby

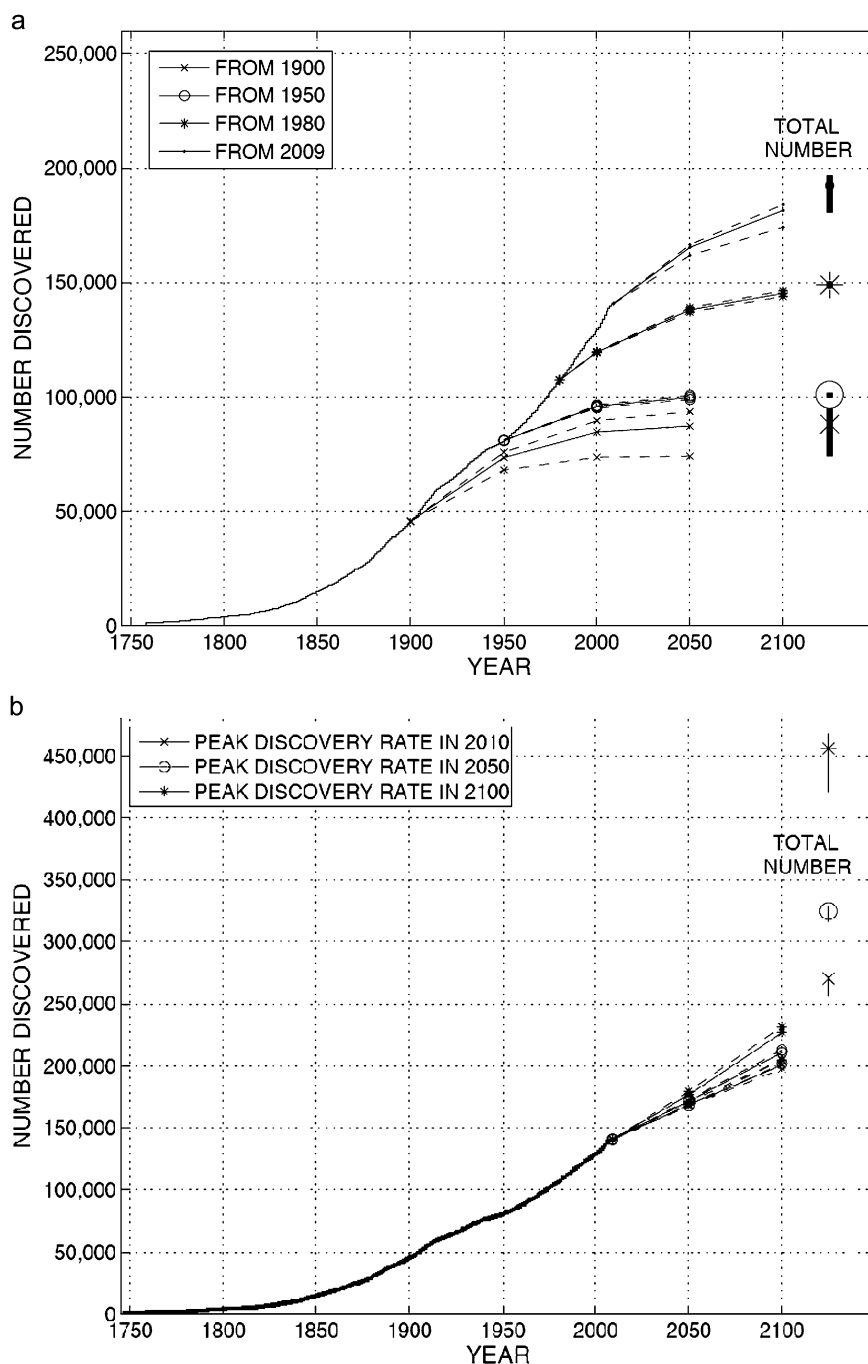


FIGURE 4. The cumulative number of marine species described over time (black line), with the total number of species predicted indicated to the right including its 95% confidence interval (vertical lines). Upper panel: The predicted number of species based on the number of species described until 1900, 1950, 1980, and from 2009. Dashed lines show 95% confidence intervals. Predictions using earlier years of description significantly underestimated the number of species later discovered. Lower panel: The predicted number of species predicted by the NHRP model assuming a peak rate of discovery in 2010 (x), 2050 (o), and 2100 (*).

both the person who collected the new species, and the person who described it, are recognized as authors. The description may also involve several people, especially where a range of morphological, genetic, and perhaps other subdisciplines are involved. This finding may also, or alternatively, indicate that increasing effort is being applied to maintain the rate of discovery and

description of new species. In fact, even ignoring when several authors described one species, there were still more authors involved than pre-1960s. The increase in authors has also been found for North American fossil mammals (Alroy 2002), marine fish (Eschmeyer et al. 2010), flowering plants and land vertebrates in Brazil (Pimm et al. 2010), and flowering plants (Joppa et al.

2011). As found in the present study, Pimm et al. (2010) found that the number of species described per author was declining. These findings may indicate that it is getting harder to discover new species because the more conspicuous ones have been discovered, but the increased overall size of the scientific community globally is offsetting this and maintaining the rate of discovery. If this is the case, at some point the effort required will be such that the pool of individuals will not offset it, and there will be a rapid reduction in the number of new species discovered. This has already occurred for birds, mammals, euphausiid crustaceans, scleractinian corals, and some insects, and closer inspection of other taxa, especially at regional scales, may reveal such a pattern as well (Gaston 1991; Costello et al. 1996; Cairns 1999; Costello and Wilson 2011; Joppa et al. 2011; this study). These taxa are conspicuous by virtue of their large body size, and/or that their location is accessible to sampling or observation. Most species remaining to be described occur in the smaller invertebrate taxa (Costello et al. 1996; Wilson and Costello 2005; Stork et al. 2008; Costello and Wilson 2011). A more detailed analysis of species discovery rates with measures of conspicuousness such as body size, location, abundance, and commonness will help refine estimates of global species richness.

It was possible that the working lifetime of specialist taxonomists has changed over time. As species new to science become harder to find, one would expect authors to only describe them on an opportunistic basis and devote their time to other aspects of species biology or ecology. Thus, the increase in the number of authors describing species since the 1950s may not reflect increased scientific effort if there have been fewer people specializing in taxonomy. At present, we do not know for how long recent (since 1950) authors will continue to publish and thus whether the post-1950s author durations will be similar to previous decades. However, the facts that the average lifetime of author's surnames, the proportion of prolific authors, and skewness of authorships, did not show any trend over time indicated that there was still the same proportion of people who specialized in taxonomy to part-time taxonomists. The lower proportion of species described by the most prolific authors in recent decades may reflect the greater number of authors describing species and that authors may publish more frequently than in earlier decades (i.e., their publications may be spread more evenly across decades). It is possible that there is more effort needed to describe species nowadays due to the need to account for more species relationships and synonyms, more past literature, and higher standards in journals (Frank and Curtis 1979). However, this may be offset by more rapid access to publications and colleagues, and computerized processes for the preparation of species descriptions for publication. Thus, on balance, the large increase in the number of authors suggests that taxonomic effort has increased since the 1950s and may be part of the reason for the continued high rate of species discovery.

Marine Biodiversity

We analyzed data on 141,000 marine species. Winston (1992) estimated about 250,000 marine species were described, although her figure for molluscs was probably the total number believed to exist. Reaka-Kudla (1996) estimated that there were 1,868,000 species described in the world, of which 274,000 were marine. Gibbons et al. (1999) estimated there were 204,000 marine metazoan animals described, and van der Land (1994) 150,000. However, the most recent published estimate, similarly based on the opinions of experts in individual taxa was 230,000 (Bouchet 2006). Thus, if we assume our WoRMS data fairly represented 61% of all described marine species, then our results predict that 65,000–91,000 more marine species remain to be discovered. That is, a total of 295,000–321,000 marine species on Earth, which considering the errors involved in such estimates and that almost 2000 species are described per year, should be reported as 0.3 million. In contrast, previous estimates of marine species richness have ranged from “certainly greater than 1 and may exceed 10 million” (Grassle and Maciolek 1992), to 5 million (Poore and Wilson 1993), 0.5 million (May 1992), over 1 million (Winston 1992), and 1.4–1.6 million (Bouchet 2006). As mentioned, our predictions are conservative. However, they are still lower than all previous estimates, and closest to May's. Why such estimates vary so widely deserves further consideration.

We do not consider that the WoRMS data need adjustment to account for parasites or microbial eukaryotes because both are already included. The number of protozoans may not alter these figures significantly because at least half of all species may already be described (Foissner 2006). There is increasing evidence that many microscopic species, including phytoplankton and protozoa, but perhaps other zooplankton and benthic meiofauna, are very widespread in the oceans (Foissner 2006; Lozupone and Knight 2007; Costello et al., unpublished data). This reflects their great abundance when in a suitable environment, and low extinction rates due to life stages that can survive unsuitable environmental conditions. Microplankton and meiobenthos are easily dispersed by water currents and attached to animals. In contrast to larger animals, their dispersal is passive and without an energy cost (O'Dor et al., 2009).

One of the reasons for high estimates of undiscovered marine biodiversity reflected the lack of sampling of the largest habitat on Earth. Less than 10% of the deep sea has been mapped by ships (Charette and Smith 2010), and 60% of the planet is below 1000 m depth (Costello, Cheung, et al. 2010). Undersampling underestimates alpha (local) diversity and overestimates beta (habitat) diversity, leading to inaccurate estimates of gamma (regional) diversity (Stork et al. 2009). In contrast to early diversity–stability hypotheses of high speciation and richness in a large stable deep-sea environment, the evidence suggests this is not the case, although extraordinary species and habitats occur there (e.g., hydrothermal vents, deep-sea coral reefs). Recent evidence

TABLE 1. The predicted number of marine species based on data to 2009

N	All to 1900	All to 1950	All to 1980	All to 2009	Pisces ^a	Polychaeta ^a	Isopoda ^a	Echinodermata ^a	Aves	Mammalia	Total 6 GSD
	45,635	81,030	107,475	140,768	16,049	11,548	5866	5721	814	130	40,128
To 2050											
Mean	87,336	99,828	138,119	165,359	21,138	16,451	9540	6400	816	132	54,477
Median	87,959	99,887	138,150	165,536	21,137	16,452	9537	6523	816	132	54,597
SD	4583	5770	467	987	102	98	104	271	2	2	578
Lower	74,135	98,940	137,111	161,910	20,942	16,263	9345	5891	814	130	53,385
Upper	93,590	100,602	138,976	166,615	21,341	16,640	9741	6716	820	136	55,394
CV (%)	5.2	5.8	0.3	0.6	0.5	0.6	1.1	4.2	0.2	1.3	0.6
To be discovered by 2050											
Lower	28,500	17,910	29,636	21,142	4893	4715	3479	170	0	0	13,257
Upper	47,955	19,572	31,501	25,847	5292	5092	3875	995	6	6	15,266
To 2100											
Mean	—	—	145,300	181,575	21,154	23,656	15,650	7165	817	133	68,576
Median	—	—	145,341	181,965	28,151	23,658	15,635	7500	817	133	75,894
SD	—	—	627	2098	208	208	269	677	2	3	1367
Lower	—	—	143,943	174,158	27,759	23,254	15,171	5958	814	130	73,086
Upper	—	—	146,434	184,203	28,572	24,049	16,155	7894	822	139	77,631
CV (%)	—	—	0.4	1.2	1.0	0.9	1.7	9.4	0.2	1.9	0.9
To be discovered by 2100											
Lower	—	—	36,468	33,390	11,710	11,706	9305	237	0	0	32,958
Upper	—	—	38,959	43,435	12,523	12,501	10,289	2173	8	9	37,503
Total to be discovered											
Mean	88,137	100,956	148,959	192,443	61,098	50,478	33,302	62,637	818	135	208,468
Median	88,780	101,023	148,997	193,043	61,094	50,484	33,267	24,041	818	134	169,838
SD	4793	645	736	3294	486	482	622	123,483	2	4	125,079
Lower	74,252	99,981	147,353	180,760	60,162	49,538	32,198	5980	814	130	148,822
Upper	94,889	101,817	150,285	196,607	62,072	51,373	34,440	459,320	823	143	608,171
CV (%)	5.4	0.6	0.5	1.7	0.8	1.0	1.9	197.1	0.3	2.6	1.0
To be discovered in total											
Lower	28,617	18,951	39,878	39,992	44,113	37,990	26,332	259	0	0	108,694
Upper	49,254	20,787	42,810	55,839	46,023	39,825	28,574	453,599	9	13	568,043
% total to be discovered of number now known											
Lower	—	—	33.9	23.7	73.0	101.4	158.6	4.1	0.0	0.0	82.1
Upper	—	—	36.2	30.9	78.0	108.3	175.4	38.0	1.0	6.9	93.5

Notes: N = total number of species in present database; SD = standard deviation; CL = confidence limits; CV = coefficient of variation (% SD/mean).
^aDatabases whose predictions are doubtful for beyond 2100.

TABLE 2. The predicted total number of terrestrial species by database to 2050, to 2100, and for the total remaining species

Database name	LepIndex	Species fungorum	SpidCat ^a	OSF	Scarabs ^a	CCW	TIGR Reptile ^a	Odonata ^a	ZOBODAT	ChiloBase	ASF	Total
	Butterflies moths	Fungi	Spiders	Crickets	Scarab beetles	Crane flies	Reptiles	Dragon flies	Wasps	Centipedes	Mantids	
No. described	230,246	39,650	39,238	23,541	17,638	14,360	8609	5416	5232	3130	792	370,214
To 2050												
Mean	243,000	57,600	46,200	25,300	21,000	14,500	9900	5900	5900	3200	830	412,330
Median	242,000	57,600	46,200	25,300	21,000	14,500	9900	5900	5900	3200	830	411,330
SD	2000	430	300	285	90	14	80	50	60	10	7	3236
95% lower	240,000	56,800	45,700	24,600	20,400	14,500	9800	5800	5800	3170	820	406,990
95% upper	246,000	56,600	46,700	25,800	20,700	14,600	10,100	6000	6500	3210	840	418,350
CV %	0.8	0.7	0.6	1.1	0.4	0.1	0.8	0.8	1.0	0.3	0.8	0.8
Number to be discovered												
Lower	9754	17,150	6462	1059	2762	140	1191	384	568	40	28	36,776
Upper	15,754	18,950	7462	2259	3062	240	1491	584	1268	80	48	48,136
To 2100												
Mean	250,000	72,700	50,400	26,300	23,000	14,500	10,900	6100	6300	3200	840	441,240
Median	249,000	72,700	50,400	26,300	23,000	14,500	10,900	6100	6300	3200	840	440,240
SD	3800	1000	350	70	150	15	150	60	110	11	10	5576
95% lower	245,000	71,000	49,800	26,150	22,300	14,500	10,700	6000	6100	3180	820	433,250
95% upper	257,000	75,300	51,100	26,450	22,800	14,600	11,200	6300	6500	3230	860	452,540
CV %	1.5	1.4	0.7	0.3	0.7	0.1	1.4	1.0	1.7	0.3	1.2	1.3
Number to be discovered												
Lower	14,754	31,350	10,562	2609	4662	140	2091	584	868	50	28	62,336
Upper	26,754	35,650	11,862	2909	5162	240	2591	884	1268	100	68	82,026
Total to be discovered												
Mean	254,000	84,400	52,920	26,700	24,000	14,500	11,900	6200	6500	3200	2840	463,160
Median	252,000	84,300	52,920	26,700	24,000	14,500	11,800	6200	6500	3200	2840	460,960
SD	5500	1700	322	250	210	16	273	87	140	11	11	8310
95% lower	247,000	81,400	52,300	26,200	23,600	14,500	11,400	6000	6200	3190	820	449,010
95% upper	264,000	88,700	53,500	27,200	24,400	14,600	12,500	6600	6800	3230	860	477,990
CV %	2.2	2.0	0.6	0.9	0.9	0.1	2.3	1.4	2.2	0.3	0.4	1.8
Number to be discovered												
Lower	16,754	41,750	13,062	2659	5962	140	2791	584	968	60	28	78,796
Upper	33,754	49,050	14,262	3659	6762	240	3891	1184	1568	100	68	107,776
% total to be discovered of number now known												
Lower	7.3	105.3	33.3	11.3	33.8	1.0	32.4	10.8	18.5	1.9	3.5	21.3
Upper	14.7	123.7	36.3	15.5	38.3	1.7	45.2	21.9	30.0	3.2	8.6	29.1

Notes: Abbreviations are as in Table 1. See Supplementary Material for more details on the databases.
^aDatabases whose predictions are doubtful for beyond 2100.

across a range of taxa indicates species richness is higher in warmer climates due to higher metabolism and mutation rates generating higher rates of speciation (e.g., Martin and Palumbi 1993; Wright et al. 2006, 2011). Even if an ectothermic species adapts its metabolism to different temperatures, its populations in warmer waters will have shorter generation times thereby facilitating their differentiation from cold-water populations should there be sufficient time. In shallow seas, photosynthesis fueled productivity will produce more abundant populations, and this abundance may facilitate speciation and mitigate against extinction. In addition, most tropical seas support elaborate coral reefs that provide a physically diverse three-dimensional habitat without parallel in colder seas. By contrast, the deep sea is cold ($<4^{\circ}\text{C}$) with far lower primary productivity and habitat variation. Finally, the fossil evidence suggests generally more species evolved in shallow tropical seas (Briggs 1995), although there may be particular taxa that are more diverse in colder climates. As predicted by Ekman (1953), deep-sea species have greater distribution ranges than shallow water species (e.g., Macpherson 2003; Fortes and Absalão 2010; Eschmeyer et al. 2010). In addition, species depth ranges increase with depth so there are few abyssal and hadal endemics (e.g., Rex et al. 2005; Vanreusel et al. 2010). Deep-sea populations need good dispersal abilities (and thus high gene flow) to overcome low population densities in the deep sea and to colonize isolated habitats (e.g., hydrothermal vents, whale falls) (Krylova and Sahling 2010). The fluctuations in Pleistocene sea levels may have fostered allopatric speciation along coastlines, but not in deeper seas (Clarke and Crame 2010). Apparent endemisms may reflect insufficient sampling in the oceans, especially for species that may occur in low density in suboptimal environments. Thus, deep-sea species will have larger ranges and fewer species per unit area than in coastal waters, and coastal seas less species density than on land. The midocean pelagic waters are also less sampled than coastal areas. However, these are dominated by relatively few species per unit area and they have widespread distributions (e.g., Gibbons et al. 2005; Costello et al., unpublished data).

The estimated 230,000 described marine species is 15% of all presently described species. Even accounting for the relatively higher rate of discovery underway for marine species predicted here, the oceans would still include only 16% of all species on Earth despite life originating there and its greater diversity of phyla and classes than on land. The lower richness of species in the sea than on land may be a consequence of its relatively less variable environment (with fewer physical niches that isolate populations) and organisms' greater dispersal abilities. In addition, insects, which comprise most species on earth, appear to have diversified due to the diversity of flowering plants (e.g., Novotny et al. 2006), which provide habitat structure as well as food over most of the land area. In contrast, habitat structuring plants, such as seaweeds, mangroves, and seagrasses,

only occur in the coastal rim of the ocean and provide a more limited habitat.

Recent predictions of the number of undiscovered marine species are as modest as ours. Eschmeyer et al. (2010) considered that most marine fish for the Northern Hemisphere have been described, and that it is taking more effort (authors) to discover more species. They proposed that about 5000 (30%) more marine fish species would be discovered by 2050, which is the midpoint of the range of marine fish our present model predicts will be discovered by 2050 (Table 2). In an analysis of marine species in Europe, we predicted 32% remained to be discovered (Costello and Wilson 2011). New Zealand, with the highest rate of marine endemism of any country (Costello, Coll, et al. 2010), has 12,780 described species, 6740 species undescribed in specimen collections, and an estimated 16,990 (87% of described number) that remain to be discovered (i.e., 36,550 species in total) (Gordon et al. 2010).

Comparison with the Fossil Record

In addition to many living marine species being undescribed, due to being inconspicuous by virtue of their location, microhabitat, small size, or lack of distinctive features, we must assume an even higher proportion of marine fossil species are undescribed as many will leave little fossil record. Over half (57%) of shelled molluscs, and 46% of dinosaurs, may leave no fossil record (Cooper et al. 2006; Wang and Dodson 2006). Crustaceans (which make up 20% of present marine species), and the many soft-bodied species will leave fewer fossils still. In a review, May (1994) calculated that present-day biodiversity is only 2–5% of all species that ever existed on Earth. This estimate was based on species life spans in the fossil record, which largely consisted of 250,000 marine species. It is remarkable that more fossil than recent species may have been described, although some species in the fossil record may still be extant. If the estimated 0.5–1.6 million marine species alive today are 5% of all that ever existed, then there were an estimated 10–32 million extinct species. The number of known fossil species is thus 1–2.5% of the undescribed fossil species. It seems unlikely that a smaller proportion of living than fossil species (i.e., $<2.5\%$) has been described, thus arguing against the predictions of there being over 9.2 million living marine species.

Terrestrial Biodiversity

Rather like hyperestimates of marine biodiversity, estimates of terrestrial species diversity, largely based on insects, have ranged from 5 to 100 million (reviewed by Hamilton et al. 2010). It has been estimated (there is no register) that there are about 1 million insects described and 2–5 million may exist (reviewed by Gaston 1991; Dolphin and Quicke 2001). Two statistical models of tropical beetle diversity considered that about 76–94% may await description, and between 6.1 or

7.8 million tropical arthropods may exist (Hamilton et al. 2010, 2011). However, the 95% confidence limits over both models ranged from 3.6 to 13.7 million, and determined that earlier extrapolations of over 30 million tropical arthropod species were highly unlikely. A review of knowledge of insect families found about 350,000 described species of beetles, and suggested 1–3 million insect species may exist (Gaston 1991), whereas extrapolation from Sulawesi rain forest Hemiptera suggested there may be 1.84–2.57 million insects globally (Hodkinson and Casson 1991). These estimates of insect diversity may be too high because most insects have good dispersal abilities, large geographic ranges, and high rates of synonymy (Gaston 1991; Gaston and Mound 1993). The 370,000 terrestrial species analyzed in the present paper thus comprised about 22% of the estimated 1.3 million described terrestrial species, and we predicted 21–29% more species remained to be discovered. Pimm et al. (2010) and Joppa et al. (2011) also included taxonomic effort in their estimates of diversity and predicted only 1% of birds, 6% of mammals, 15% of amphibians, and 16.5% of plants in Brazil; and 10–20% more plants globally; awaited discovery. If our findings are representative of all terrestrial and freshwater species, our analyses indicate that 0.27–0.37 million more remain to be discovered. This sums up to a total of 1.6–1.7 million potential terrestrial species. Adding the predicted 0.3 million marine species, our data and analyses suggest that there may be 1.8–2.0 million species on Earth. Even excluding consideration of synonyms in a recent estimate of 1.9 million described species (Chapman 2009) would predict 2–2.1 million species on Earth. These are lower than previous estimates and invite further research. This research may include accounting for taxonomic effort, rates of synonymy, and how conspicuousness species are by virtue of their size, location, commonness, or other features, in statistical models.

Outlook

This study provides a broad context for more detailed analyses of past, current, and future discoveries by specialists in particular taxa. Our predictions may have overestimated future discoveries if, (i) the continued high rate of species description, at about 18,000 species per year (Wheeler and Pennak 2010), including about 2000 marine species per year, was due to increased taxonomic effort since the 1950s, and (ii) delays in recognizing and resolving synonyms. On the other hand, our predictions may be underestimates due to the data being biased toward better known taxa in better studied geographic areas, and the conservative properties of the statistical model. The higher rate of species discovery in the oceans suggests it has been getting relatively harder to discover new species on land. Nevertheless, the results suggest that about two-thirds of all species have been described. Bouchet (2006) estimated it would take 250–1000 years to describe all species on Earth, and noted that the rate of description of new species

of marine animals was less than the rate for terrestrial when adjusted for the lower richness of described marine species. However, if our predictions are proven true, it will soon become harder to find species new to science except among the smaller invertebrates in the less explored areas and habitats, and the description of most species on Earth would be a feasible goal this century. Achieving this will be expedited by international collaboration to (i) share taxonomic knowledge through online databases (e.g., May 1998; Appeltans et al. 2010), (ii) fill geographic, habitat, and taxonomic gaps, and (iii) publish identification guides online to increase the pool of people able to discover new species (Costello, Coll, et al. 2010). Putting better numbers to the described species, and what taxa and places undescribed species will occur, will help estimate both world biodiversity and extinction rates (Gaston and Mound 1993; May 1998; González-Oreja 2008; Stork et al. 2009; Stork 2010; Joppa et al. 2011). Completing the inventory of known species is thus a priority for both biodiversity data management and conservation.

SUPPLEMENTARY MATERIAL

Supplementary material, including data files and/or online-only appendices, can be found at <http://www.sysbio.oxfordjournals.org/>.

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