

Pattern as observation: Darwin's 'great facts' of geographical distribution

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ABSTRACT. Among philosophical analyses of Darwin's *Origin*, a standard view says the theory presented there had no concrete observational consequences against which it might be checked. I challenge this idea with a new analysis of Darwin's principal geographical distribution observations and how they connect to his common ancestry hypothesis.

1 Introduction

The simplest and most fundamental approaches to testing theories require the theory to tell us what we should expect to observe in nature were that theory correct (or more generally, how *probable* some observations would be, were the theory correct). But according to most philosophical analyses, the theory Darwin put forward in *Origin of Species* falls short of this standard. Were it true, as Darwin claimed, that all species trace back to one or a few common ancestors, and that natural selection is the primary means of modification, it wouldn't follow that tigers should have stripes, that grasses should have a wide geographical distribution, or that beetles should be so prolific. As Kitcher (1985) diagnoses the problem, the relation between Darwin's theory and any observation is 'doubly loose', since neither does the theory dictate the historical trajectory (genealogical, geographical, ecological) of any particular species or group, nor do hypotheses

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about such historical trajectories always tell us what we should expect to observe in the present.

This apparent shortcoming introduces an interpretive problem that all philosophical commentators must face. How can Darwin have made a good scientific argument for his theory without having compared what actually obtains in nature with what *should* be observed were his theory correct? The literature offers a variety of solutions. Darwin's theory is said to *explain* the observations collected in the *Origin*, where the 'explains' relation is left unanalysed (Thagard; 1978; Recker; 1987; Hodge; 1991; Waters; 2003), or to *fit* the observations *after post hoc adjustment*, where the assumptions used in the fitting are testable in principle (Lloyd; 1983; Recker; 1987), or, similarly, to *provide a framework* within which speculative, yet ultimately testable, historical narratives (leading up to an observed event) can be formulated (Kitcher; 1985, 1993, 2003). Darwin's theory is then said to compare favourably with the alternatives in virtue of one or more of the following: the *number* of observations it can explain (or can be made to fit, or about which a story can be told), the number of *different kinds* of observations explained, the *novelty* of these kinds, the prior plausibility or familiarity of the *causes* cited in the explanations (*vera causa*), and the *economy* with which the theory does so much explaining.

Contrary to the premise of the interpretive problem posed above, I will argue that Darwin's theory, as presented in the *Origin*, did have straightforward observational consequences and that some of Darwin's key observations report specific facts that line up with what the theory says. While the analyses cited above each illuminate aspects of Darwin's long and complicated argument, they misrepresent how Darwin's theory relates to (at least some of) his supporting observations (and consequently, how those observations might be said to support the theory).

The observations I have in mind are large-scale *patterns* observable in nature. Existing philosophical analyses manage to describe how Darwin's theory relates to these broad, 'high-level' observations only by breaking them down into smaller constituent observations and describing how the theory relates to each of the bits. While the relation to each of the bits is indeed loose, I put this result down to an *infelicitous decomposition* of the large-scale pattern into the bite-sized observations. The innovation in my analysis is a novel decomposition that works not by chopping the big-picture observation into bits, but rather by disentangling the pattern from the irrelevant details and then treating the pattern itself as the observation.

Specifically, I will address the biogeographical patterns discussed in the opening pages of Darwin's two chapters on geographical distribution. I will first describe and unpack those observations, then attempt to derive them—or rather, the pattern they instantiate—from Darwin's theory. This derivation (qualitative, not numbers and proofs) will not require all of Darwin's theory; one part will do all the work, namely, Darwin's main conclusion in the *Origin*: that diverse species share *common ancestry* (Darwin; 1859/2003, 6). Darwin's secondary conclusion, that 'Natural Selection has been the main but not exclusive means of modification'

(6) will have little to do here.

As my analysis of Darwin's biogeographical observations will exemplify a more general point about how hypotheses can connect to observations, I first introduce the general point with a simple coin example.

2 A warm-up example

Suppose you receive two data sets, α and β , each reporting the outcomes of fifty coin tosses. And suppose I tell you my hypothesis about the process that generated those data: a single coin was tossed one hundred times, and α and β record outcomes 1–50, and 51–100, respectively. My hypothesis is silent on whether the coin is fair or biased; the chance of heads could be anywhere between zero and one (but whatever it is, it is constant, and each toss is independent of the others). Can my hypothesis be checked against these data?

Say the first entry in α is 'heads'. How likely is this? My hypothesis does not answer this question. Loosely speaking, it *doesn't say enough* to do so. The same goes for any individual entry in either data set. What about some more abstract features of the data, such as the *frequency* of heads in α ? This too depends on the coin's unknown probability of landing heads. And the same for the frequency of heads in β , and in the total data α plus β . But consider an even more abstract feature: the *difference* between the frequency of heads in α and that in β . My hypothesis says that both data sets were generated by tossing *the same coin*, so the frequency of heads in the two data sets should be roughly the same. This prediction holds regardless of the coin's (unknown) probability of landing heads.¹

The moral of the story is that a hypothesis with nothing to say about any individual observation can yet stick its neck out when it comes to more abstract or 'high level' features of a set of observations. While familiar to statisticians, this point is less well appreciated by philosophers of science and has been largely overlooked in philosophical analyses of Darwin's argument in the *Origin*. Darwin's theory doesn't tell us what to expect when it comes to individual observations about a particular species' morphology or whereabouts. But it is a mistake to think that because the hypothesis makes no predictions about these 'lower-level' observations that it makes none about any 'higher-level', or comparative statements about collections of such observations.²

¹The probability distribution assigned to the statistic $|frequency_\alpha - frequency_\beta|$ by the binomial model for the total data set (that's the technical name for my hypothesis) does depend on the coin's probability (θ) of landing heads (*i.e.*, the statistic is not quite ancillary). But for all θ , 0 is most probable and values greater than 0.2 are extremely improbable. This theory-observation relationship can also be described in terms of a good cross-validation score (Forster; 2007) across a partition of the full data set into parts α and β .

²The example and lesson are adapted from Forster's (1988) study of astronomical observations vis-à-vis Newtonian mechanics. Also compare Sober's (2008, 219) discussion of 'shifting the explanandum' from single trait values to cross-species correlations when testing for adaptations.

3 Geographical distribution

Darwin opens chapter eleven with a pithy, big-picture review of what's known about the geographical distribution of living species. As Darwin sees it, the key observations can be condensed into three 'great facts':

The first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions. (346)

A second great fact which strikes us in our general review is, that barriers of any kind, or obstacles to free migration, are related in a close and important manner to the differences between the productions of various regions. (347)

A third great fact, partially included in the foregoing statements, is the affinity of the productions of the same continent or sea, though the species themselves are distinct at different points and stations.³ (349)

A page or two of discussion follows each fact, including a number of examples. To illustrate the first of these facts, Darwin writes (see Figure 1):

In the southern hemisphere, if we compare large tracts of land in Australia, South Africa, and western South America, between latitudes 25° and 35°, we shall find parts extremely similar in all their conditions, yet it would not be possible to point out three faunas and floras more utterly dissimilar. (347)

What the example shows is that regions similar in terms of climate and physical conditions need not host similar biotas. Darwin continues:

Or again we may compare the productions of South America south of lat. 35° with those of north of 25°, which consequently inhabit a considerably different climate, and they will be found incomparably more closely related to each other, than they are to the productions of Australia or Africa under nearly the same climate. (347)

Now Darwin has expanded the comparison by introducing a *contrasting* climate within South America. Among the four regions compared, the most 'closely related' biota occupy the *mismatched* climates, not the similar ones. So the first fact is reporting that when comparing regions, similarity of climate has no bearing on similarity of biota. (I will shortly address what is meant by 'similar' or 'closely related' biota.)

In this example, the two South American regions are physically close to one another. Is this important? Yes it is: the second great fact reports that barriers

³See Nelson (1978) for discussion of these observations (especially the first) in the work of Darwin's contemporaries and predecessors, including Linnaeus, Buffon, Candolle, Prichard, Humboldt, and Lyell.

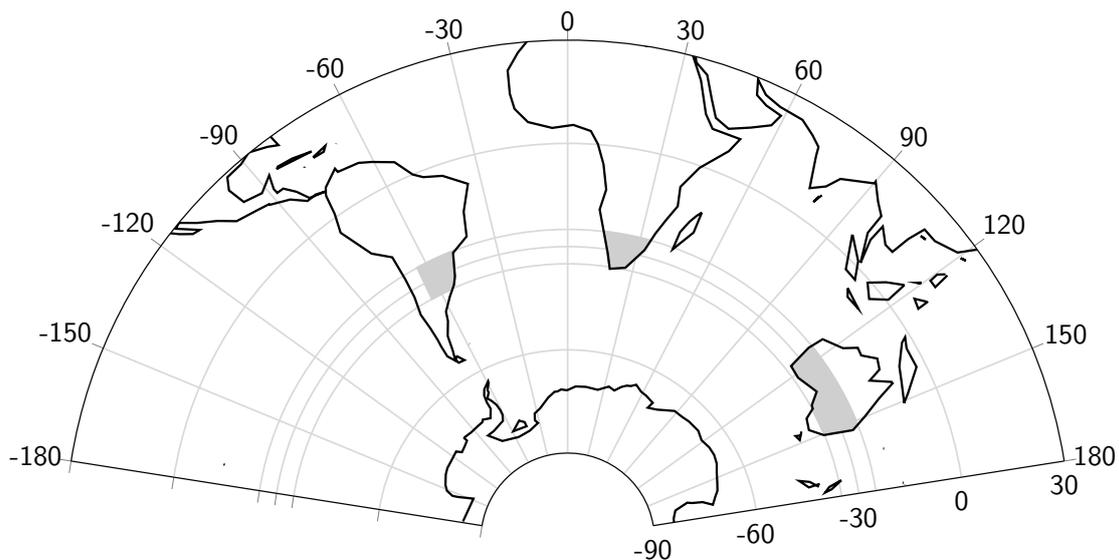


Figure 1: A map illustrating three regions of the Southern Hemisphere between latitudes 25° and 35° ; similar environments but contrasting flora and fauna.

to migration are ‘related in a close and important manner’ to differences between regional biotas, which Darwin clarifies by noting the ‘great difference in nearly all the terrestrial productions of the New and Old worlds’ and ‘between the inhabitants of Australia, Africa, and South America under the same latitude: for these countries are almost as much isolated from each other as is possible’ (347). The same goes for marine fauna separated by ‘impassable barriers, either of land or of open sea’ and to a lesser degree, for regional biota separated by ‘lofty and continuous mountain ranges, . . . great deserts, and sometimes even large rivers’ (348). The greater the barriers that separate two regions, the greater the differences between their inhabitants.

The other side of the same coin is the similarity of inhabitants at different points within an area undivided by barriers and therefore open to free migration. These areas tend to coincide with the continents, or for marine life, the seas, and thus the third great fact: ‘the affinity of the productions of the same continent or sea’.

All together then, the three great facts say roughly the following. When comparing the inhabitants of one region to those of another, more similar biota inhabit regions that are more accessible through migration or dispersal, regardless of differences in climate and physical conditions.

3.1 Similarity of inhabitants

But what does it mean to say the living things (‘inhabitants’, ‘productions’) of one region are similar or dissimilar to those of another? How can such miscellaneous

collections be compared? One approach might be to judge similarity by the number of species two biotas have in common. But Darwin goes beyond this to recognise similarity where ‘the species themselves are distinct’ (349). I read him as judging two biotas similar to the degree that species found in one tend to be matched by *similar species* in the other. In terms of an everyday example, two sets of cutlery are similar since the fork in one looks much like the fork in the other; the same for the spoon, the knife, and so on. In contrast, a set of hand tools is relatively dissimilar, since a spanner is a strange looking fork, and a screwdriver a rather dull and slender knife.

This first-pass analysis reduces similarity between biotas to similarity between species, but what is *species* similarity? Darwin’s use of the terms ‘affinity’ (349) and ‘related’ (349), as well as the phrase ‘species of the same genus’ (349) indicate that he is thinking in *taxonomic* terms. The groups-within-groups structure of biological classification partitions taxa into mutually exclusive groups, with each group itself divided into subgroups, and so on for the subgroups.⁴ Groupings can be written out using brackets, for example, $((human, chimpanzee) orangutan)$ means that humans and chimps are each taxonomically closer to each other than to orangutans. Such classifications express *relative* taxonomic relatedness—which is closer to which—without saying *how closely* related the species are in any absolute sense. (Taxonomic ranks such as *family* and *genus* appear to offer an *absolute* yardstick for relatedness, but Darwin dismisses these ranks as arbitrary.)

So when Darwin says that the inhabitants of neighbouring regions of South America are ‘incomparably more closely related to each other, than they are to the productions of Australia or Africa,’ I take him to mean the following. Pick any species from the one South American region, and then identify its closest taxonomic relatives found in the other South American region and in the mooted regions of Australia and Africa. Label the species *sa*, *sa**, *au* and *af*. With some exceptions, the taxonomic relations among species selected in this way will generally be $(sa, sa^*) au$ and $(sa, sa^*) af$. On this reading, each of Darwin’s statements about the relative similarity of the ‘inhabitants’ of different regions can be understood as a summary of many smaller-scale facts about the *taxonomic relations* among representative species drawn (as described above) from the biotas of those regions.

⁴O’Hara (1991) divides taxonomic representations in the forty years prior to publication of the Origin into the Quinarian (1819–1840), and mapmaking (1840–1859) periods. While there is considerable diversity within each period, the primary structure in both is the nested grouping as explained in the text. Quinarian classification requires exactly five subgroups within every group and includes additional relationships that cross-cut the nested groupings. Some of what O’Hara calls ‘maps’ also include supplementary cross-cutting relationships.

3.2 Flightless birds, rodents

While Darwin discusses the great facts mainly in terms of the biota comparison language that I have just interpreted, he also gives two examples at the more detailed level of representative taxa. First example:

The plains near the Straits of Magellan are inhabited by one species of Rhea (American ostrich), and northward the plains of La Plata by another species of the same genus; and not by a true ostrich or emeu, like those found in Africa and Australia under the same latitude. (349)

What is now called *Darwin's rhea* inhabits the arid southern-most plains of South America, while the *greater rhea* inhabits the plains somewhat to the north, in a nearby region with a different climate. Their closest taxonomic relatives found in corresponding regions of Africa and Australia are the ostrich and emu, respectively (see Figure 2).

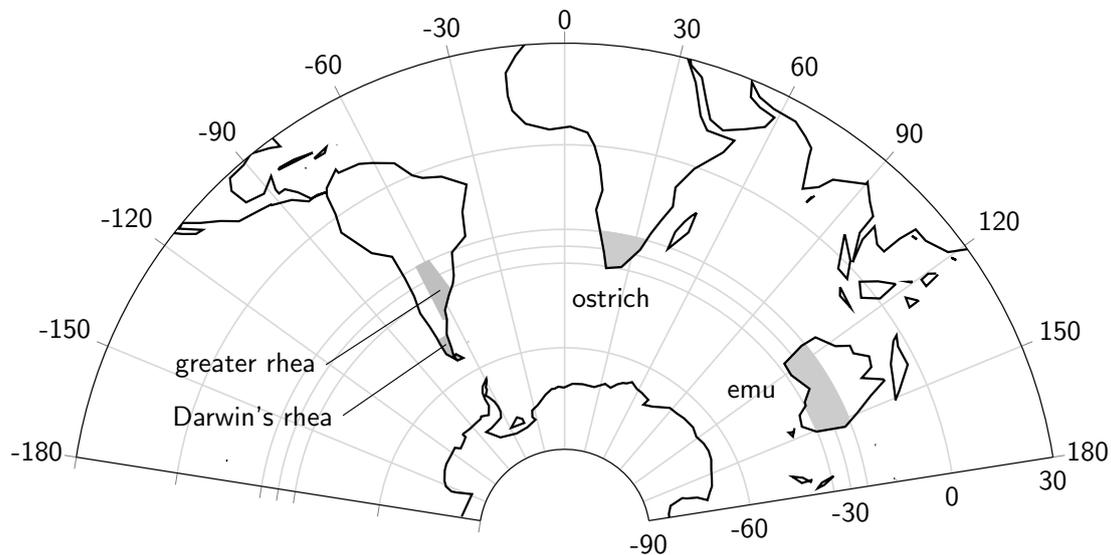


Figure 2: A map illustrating Darwin's flightless birds example; the two species of rhea are geographical neighbours as well as close taxonomic relations.

The two rheas are taxonomically more closely related to each other than either is to the ostrich or the emu: $(rh, rh)_{os}$, and $(rh, rh)_{em}$. And the *regions* inhabited by the two rheas are geographically more accessible to each other than either is to Australia or southern Africa. The relative accessibility between regions is thus mirrored in the taxonomic relations between closely related species that inhabit those regions.

This is what the great facts look like when viewed in terms of particular species. More precisely, the taxonomic relations between the rheas, ostrich and emu show one instance of the general trend of closest taxonomic relations from accessible

regions being more closely related than those inhabiting relatively inaccessible regions (regardless of similarity/disimilarity between regional environments). Many such instances, featuring the same four regions, are summarised in Darwin’s statement that the ‘productions’ of neighbouring South American regions are ‘more closely related to each other, than they are to the productions of of Australia or Africa under nearly the same climate’.

Darwin’s second ground-level example addresses a group of South American rodents and their more widely dispersed taxonomic relatives:

On these same plains of La Plata, we see the agouti and bizcacha, animals having nearly the same habits as our hares and rabbits and belonging to the same order of Rodents,⁵ but they plainly display an American type of structure. We ascend the lofty peaks of the Cordillera and we find an alpine species of bizcacha; we look to the waters, and we do not find the beaver or musk-rat, but the coypu and capybara, rodents of the American type. (349)

You might have thought, says Darwin, that South American lakes and rivers would hold beaver or muskrat as in Europe and North America; but instead we find the coypu or capybara (depending on the region), which are taxonomically more closely related to each other and to neighbouring rabbit-like rodents, the agouti and viscacha: $(ago, vis, coy, cap) bea, mus$.⁶ Comparing the regional rodents of South America to Europe’s hares and rabbits gives the same result: $(ago, vis, coy, cap) har, rab$.

The point, as in the previous example, is that closest taxonomic relatives found in neighbouring, accessible regions are *more closely* related than those found in inaccessible regions further afield—in this case North America and Europe. Here Darwin has chosen the example to further illustrate the robustness of this generalisation: it holds up despite coypu and capybara sharing a *station* (roughly, an ecological niche) with the beaver and muskrat, and despite agouti and viscacha having nearly the same *habit* (superficial external appearance) as hares and rabbits. He adds, concerning South America, that ‘Innumerable other instances could be given’, and more broadly, ‘It is a law of the widest generality, and every continent offers innumerable instances’ (349).

⁵Rabbits and hares were moved out of *Rodentia* and into the sister order *Lagomorpha* in the early 20th century. This development doesn’t undermine Darwin’s argument. (There are closer taxonomic relations in Europe and America, but these are still taxonomically more distant than the South American rodents are to each other.)

⁶Partial classifications such as $(abcd)ef$ leave open where additional groupings should go, and can be read as disjunctions of all compatible group structures. In this case, the ef could be further specified as $(\cdot)(ef)$, $((\cdot)ef)$, or $((\cdot)f)e$, and the internal structure of $(abcd)$ could be any of fifteen possibilities, e.g. $((ab)(cd))$, $((ad)(bc))$, or $((a(bcd)))$.

3.3 Explanation

What is the significance of the great facts? Darwin initially makes no comment on the irrelevance of environment, though he later leverages this point against what he calls the ‘theory of creation’. His immediate concern is instead the observed association between taxonomic relatedness and geographical accessibility. Speaking of the ‘bond’ connecting species within the same continent or sea, or otherwise inhabiting regions easily accessible by migration, Darwin says, ‘This bond, on my theory, is simply inheritance, that cause which alone, as far as we positively know, produces organisms quite like, or, as we see in the case of varieties nearly like each other’ (350).

Darwin’s theory thus provides, loosely speaking, an *explanation*: geographical proximity (accessibility) and taxonomic similarity go together because both are consequences of *recent common ancestry*. What I aim to show next is that this connection between accessibility and taxonomy is not merely something that Darwin’s theory can accommodate, or make sense of, after the fact, with supplemental *ad hoc* posits and assumptions. Rather, this trend is to be expected given Darwin’s common ancestry hypothesis. (Darwin’s own language grows equally bold later in chapter 12, when he says, regarding inhabitants of Galapagos islands being more closely related to those of other islands in the archipelago than to inhabitants of any other part of the world, that ‘this is just what might have been expected on my view’ (418). This fact about the Galapagos is just another instance of the geography–taxonomy pattern described by the great facts.)⁷

4 Darwin’s hypothesis

Darwin’s common ancestry hypothesis says that all living things trace back to at most a handful of original species. But this, I will argue, is not all that it says. To understand the additional content, we must delve a bit deeper into the topic of taxonomy.

Groups-within-groups classifications like those seen above express relative taxonomic ‘relatedness’, but what does that really mean? What is classification ultimately *about*? Minimally, a given classification was both a summary of observed morphological similarities, and a predictive hypothesis regarding similarities in traits not yet observed, or not taken into account in making the classification. Beyond this superficial agreement, different naturalists had different ideas about the true nature of taxonomic relations. Gazing at a taxonomy, some saw a creator’s blueprint, others, a map of the physiologically possible adult forms, or of the constraints inherent in the process of embryological development (Winsor; 2009). Yet others saw a *genealogical tree*—at least at the lowest taxonomic ranks: varieties within a species, and perhaps even species within a genus.

⁷For further instances of Darwin’s ‘might have been expected on my theory’ language within his discussion of geographical distribution, see pages 408 and 419.

Despite these differences, taxonomists' methods were similar enough *operationally* that they could and often did agree on how to classify, even while disagreeing about the ultimate meaning of the classification. As Winsor (2009, 44) explains, 'To us it may seem paradoxical that naturalists should use the word "related" without agreeing on its meaning, but actually this tolerance enabled them to make progress as a scientific community.' Think of ethical claims in philosophy today: two philosophers can agree that 'murder is wrong', even while entertaining different theories about what it means for an act to be wrong. They agree on an ethical claim while disagreeing about meta-ethics. Naturalists before Darwin could and often did agree on classification claims even as they disagreed about (so to speak) meta-classification.

To further explore the genealogical interpretation, note that every groups-within-groups classification can also be represented, without loss of information, as a branching tree structure (Figure 3). Most naturalists already believed that subgroups within the same species were related genealogically; in terms of the tree representation, this means that some forks at the very tips of the branches were taken to indicate genealogical relations. Nodes deeper in the tree, however, were given one of the other interpretations. Darwin took the genealogical interpretation and pushed it *all the way down the tree*. All (or almost all) living things are related by genealogy, he said, and the closer the taxonomic relation, the more recent the shared ancestor.

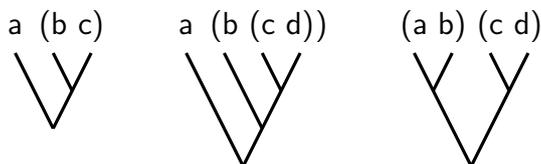


Figure 3: Example classifications and their corresponding (rooted) trees.

Darwin's common ancestry hypothesis is best understood as an *interpretation* of taxonomic relations, namely the genealogical interpretation just presented. The hypothesis says that all living things trace back to one or a few common ancestor species, that the ancestry of life has the form of a branching tree, and that the shape of this tree is revealed (at least approximately) in the taxonomic classifications of Darwin's time.

4.1 Deriving the observations

Darwin's view of taxonomic relations goes together with treating the *practice* of taxonomy as a (disguised) method of what is now called *phylogenetic inference*, or inferring the genealogical tree for a set of taxa. Indeed, the practice was largely accurate as a method of phylogenetic inference (assuming the results of today's molecular-based methods are not too far off the mark). As I will now show,

the *geography* side of the great-facts observations can be given a phylogenetic gloss as well. This new perspective will illuminate the connection between those observations and Darwin’s common ancestry hypothesis.

The association between geography and taxonomy expressed by the great facts consists of innumerable instances of the pattern seen in the cases of the rodents and flightless birds, in which taxonomic relations among species mirror the geographical accessibility of the regions they inhabit. The *geographical* observations included within any instance of this pattern can be summarised by grouping together the accessibly-located species, and applying the bracket notation used above to express taxonomic relations. In the case of the flightless birds, for example, this gives: $(rh, rh) os, em$.

This grouping approach to summarising geographic accessibility relations is formally the same as applying a simple method of *tree construction* (e.g. neighbour-joining, or UPGMA) to a matrix of pair-wise genetic or character ‘distances’ (Table 1). By another application of the one-to-one correspondence between nested groupings and branching trees, we can view the geography-based grouping procedure as a second method of *phylogenetic inference*. I will address the method’s reliability shortly, but as a first step, note that it does have a sound rationale: species that split further in the past have had more time to disperse further apart, while species that split more recently can’t have gotten too far apart since speciation.⁸

	emu		
5		ostrich	
5	5		Darwin’s rhea
5	5	1	greater rhea

Table 1: Pairwise migratory accessibility (using cartoon numbers) arranged to display the formal identity with a matrix of pair-wise character ‘distances’.

The pattern observed in the cases of the rodents and flightless birds can now be described as *agreement* between taxonomic and geography-based groupings for the same set of species. In the case of the flightless birds, taxonomy and geography agree on the placement of the two rheas within a subgroup of their own (Table 2). In the case of the rodents, they agree on the placement of the agouti, viscacha, coypu, and capybara into a subgroup that excludes beaver, muskrat, hares and rabbits.

And having given a phylogenetic, or genealogical, interpretation to *both* the taxonomic *and* the geography-based groupings, there is now a simple reason why

⁸For a more formal argument, see Sober’s probabilistic reconstruction (Sober; 2008, 326) of Darwin’s ‘space-time principle’ (Darwin; 1859/2003, 410).

taxonomy: ((Darwin's rhea, greater rhea) emu) ostrich
geography: (Darwin's rhea, greater rhea) ostrich, emu

Table 2: Agreement between taxonomic and geography-based groupings for a set of species. ‘Innumerable instances’ of this pattern add up to the trend reported by the ‘great facts’ of geographical distribution.

the agreement seen in Table 2 should be the rule and not the exception. On Darwin’s theory, these two ways of grouping should generally come to the same result because they are in fact two approaches to estimating the very same thing: the true genealogical tree for the species in question.

But is geography-based tree construction really a workable method of phylogenetic inference? After all, geographical accessibility is typically a dreadful proxy for genealogical relatedness. For example, the American bison is much more closely related to the Asian water buffalo than to the rodents, birds, grasses, and ants in its own environment. For almost any choice of taxa, judging genealogical relatedness based on geographical accessibility would do no better than putting all possible trees into a hat and reaching in blindfolded.

While grouping by geographic accessibility is indeed a very limited method of phylogenetic inference, there is a narrow set of circumstances under which it can succeed. Geographic distribution contains information about genealogical relations, but the world is small and migration is fast. The noise of dispersal quickly obscures the signal of genealogy.⁹ Geographical accessibility will be most informative about genealogy where speciations have occurred recently (on an evolutionary time scale), such that dispersal has yet to fully shuffle species’ locations. And differences in accessibility between the regions that species occupy will be most justifiably attributed to speciation order (rather than to accidents of dispersal) where those differences are *great*.

Not accidentally, both conditions are satisfied in the range of cases comprised by Darwin’s great facts. Darwin’s biota comparison statements each summarise innumerable smaller-scale, species-specific observations of the type exemplified by the rodents and flightless birds, each of which concerns a set of species that are each other’s *closest taxonomic relatives* native to the regions in question. On the genealogical interpretation of taxonomic relations, this means that all speciations will have been relatively recent, satisfying the first condition. And Darwin’s focus on contrasting regional biotas within the same continent or sea with those on separate continents or seas ensures that differences in geographical accessibility between compared regions will be very great, satisfying the second condition.

Thus the way in which the regions are chosen for comparison, and then the way in which representative species are chosen from those regions, works to restrict

⁹Somewhat more formally, and supposing that daughter species disperse via probabilistically independent random walks, the likelihood function over possible trees flattens quickly.

circumstances to those under which geographical distribution is most informative about genealogical relations. And even under these favourable circumstances, geography-based tree-construction need not be terribly reliable. It must only be reliable enough to *typically* agree with the anatomy-based taxonomic trees in the limited sense that same-continent species will belong to a taxonomic subgroup that excludes their different-continent cousins. It then follows from Darwin's genealogical interpretation of biological taxonomy that regional biotas from neighbouring, or geographically accessible, regions will be, as Darwin reports, more 'closely related' than either is to a third, geographically isolated biota. If we can use 'predicts' in the atemporal sense, then Darwin's theory predicts this observation.

4.2 Analogy with the coin example

I began by suggesting that the standard view about Darwin's theory having no concrete observational consequences flows in part from misplaced attention to overly specific, 'low-level' observations rather than 'higher-level' patterns of such observations. And I presented the coin example to illustrate a particular way in which a theory can renounce all commitments about the former and yet stick its neck out regarding the latter. Now I clarify the analogy between the coin example and Darwin's biogeography observations.

Recall that because the single-coin hypothesis says nothing about the coin's bias, it suggests nothing about the outcome of any single toss of the coin, nor about the frequency of heads in either of data sets α or β . It does, however, predict that the frequency of heads in α and β should be roughly the same, because the underlying bias of the coin, whatever it is, is constant across the two data sets. Indeed, the frequency of heads in α and in β each constitute a best (maximum likelihood) estimate of that bias.

The geography-based grouping operation sketched above can be thought of as a statistic summarising the geographical distribution observations for a set of species. Similarly, taxonomic practice can be viewed as a set of operations applied to comparative morphology observations and producing a summary statistic of the species' morphology. The 'highest-level' observation is then the agreement between these two groupings; this is the analogue of similar frequencies of heads observed in data sets α and β .¹⁰ And like the two frequencies vis-à-vis the single-coin hypothesis, the taxonomic and geography-based groupings can, on Darwin's common ancestry hypothesis, be interpreted as two estimates of a single theoretical entity posited to underly both data sets.

Viewing any given species *in isolation*, Darwin's theory has nothing to say about where it should be found on the globe, or what morphological characteristics it should display. Backing up to take in the geographical distribution of a whole collection species, the theory makes no commitment on their locations or

¹⁰Quantitative measures of tree similarity (Robinson and Foulds; 1981; Penny et al.; 1982; Penny and Hendy; 1985) might allow for an even tighter analogy.

even relative positions, *if geography is viewed in isolation from morphology*. But the *comparison* of taxonomic and geography-based trees leaves behind all of these details that go beyond the theory's commitments, to find a more abstract, comparative feature of the total morphology-plus-geography observation set about which the theory takes a stand.

From a logical point of view, the step from a full set of geography and morphology observations to a summary statement that merely reports agreement between geography- and morphology-based groupings involves a *logical weakening*. The total observations entail the agreement statement, but not the other way around. This is what explains the newfound connection between theory and observation: the theory doesn't say enough to comment on the full observations in all their richness, but by logically weakening the observations, their content is trimmed back to the bigger-picture relational features on which the theory speaks. (The alternative strategy, and the one employed in other commentaries on the *Origin*, is to forge a connection between theory and observation by *logically strengthen the hypothesis*, by adding to it extra posits and assumptions, so that its consequences expand to include the specific, local observations.)

5 Conclusion

I have offered a new analysis of the principal observations cited in Darwin's treatment of geographical distribution in the *Origin*, and of how those observations relate to Darwin's theory. My analysis challenges the conventional wisdom that his theory does not, on its own, tell us what we should expect to observe in nature were the theory correct. The novelty of my analysis comes from a re-examination—in the light of the coin example—of the biogeographic trend expressed by what Darwin calls the 'great facts' of geographical distribution. Too much emphasis on the geographical trajectories of particular species makes Darwin's theory appear vacant or overly flexible. On my reading, the key observation is the pattern, repeated across regions and environments, of agreement between taxonomic and geography-based groupings for appropriately chosen groups of species.

This has not been an assessment of how or how much the analysed biogeographical trend supports or confirms Darwin's theory, nor how it fits into his overall argument running through the *Origin*. I have focussed on the form and content of Darwin's observations rather than on particular philosophical theories of evidence or confirmation. That said, the relatively direct connection revealed here between Darwin's theory and observations does remove some of the motivation for the more *indirect* approaches to justifying or rationalising Darwin's argument cited above in my introduction. And the fact that natural selection has remained idle in the preceding analysis should encourage readings of Darwin's argument on which much of his evidence supports common ancestry without weighing in on the mechanism of evolution (Waters; 2003; Sober; 2011) over treatments that see

Darwin building a case for a single, undecomposed theory (Hodge; 1992; Recker; 1987; Sintonen; 1990; Lloyd; 1983; Thagard; 1978).

My analysis also places Darwin's observations in the context of modern evolutionary biology by framing and conceptualising the great facts in a way that allows for application of a familiar label. The agreement between genealogical trees inferred from different data sets will be recognised by contemporary evolutionary biologists as a form of *phylogenetic congruence*, as used in contemporary phylogenetic systematics (Huelsenbeck et al.; 1996), historical biogeography (Wiley; 1988), symbiotic evolution (Funk et al.; 2000), and several other subfields. The congruences discussed here, however, are different in that the second tree is based on geographical accessibility, whereas modern instances of phylogenetic congruence compare two trees each based on intrinsic features of the organisms, either morphology or genetic data.

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