



# The evolutionary contingency thesis and evolutionary idiosyncrasies

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## Abstract

Much philosophical progress has been made in elucidating the idea of evolutionary contingency in a recent re-burgeoning of the debate. However, additional progress has been impaired on three fronts. The first relates to its characterisation: the under-specification of various contingency claims has made it difficult to conceptually pinpoint the scope to which ‘contingency’ allegedly *extends*, as well as *which* biological forms are in contention. That is—there appears to be no systematic means with which to *fully specify* contingency claims which has led to a tendency for authors to talk past each other. Secondly, on the matter of evidence, recent research has focused on the evidential import of (genuine) convergent evolution which is taken to disconfirm the evolutionary contingency thesis. However, there has been a neglect of convergent evolution’s converse: ‘evolutionary idiosyncrasies’ or the *singular* evolution of certain forms, which I argue is evidentially supportive of evolutionary contingency. Thirdly, evolutionary contingency has often been claimed to vary in degrees and that the debate, itself, is a matter of ‘relative significance’ (*sensu* Beatty). However, there has been no formal method of evaluating the strength of contingency and its relative significance in a particular domain. In this paper, I address all three issues by (i) proposing a systematic means of fully specifying contingency theses with the concept of the *modal range*. Secondly, I (ii) propose an account of *evolutionary idiosyncrasies*, investigate the explanations for their occurrences, and, subsequently, spell out their significance with respect to the evolutionary contingency thesis. Finally, having been equipped with the evidential counterpart to convergent evolution, I shall (iii) sketch a *likelihood framework* for evaluating, precisely on the basis of a sequence of opposing data, the strength and relative significance of evolutionary contingency in a particular domain. With this in hand, the relative observations of idiosyncrasies and convergences can be informative of the strength and relative significance of contingency in any particular domain.

**Keywords** Evolutionary contingency · Evolutionary idiosyncrasies · Convergent evolution · Modal Range · Relative significance · Chance · Unique evolution

## Introduction

The idea of evolutionary contingency has undergone a substantial resurgence in recent years with a number of contingency-theorists entertaining the modality of evolutionarily-derived biological forms. At present, there is no consensus as to what evolutionary contingency means other than to broadly suggest that certain evolved biological forms *could have been otherwise*. The suggestion is that there is an element of ‘chanciness’ (or some similar descriptor) to *which* forms would have actually evolved in the history of life. If evolutionary contingency were true, then as the story goes: had the ‘tape of life’ been replayed (from a different or the same starting point), the result would be an evolutionary menagerie bearing biological forms markedly different from the present ones. That is—instead of our ever so familiar birds, reptiles, and mammals, we would be left with forms ‘endlessly most beautiful’... should we find ourselves fortunate enough to remain.

The majority of recent papers have set out to propose etiological structures such as ‘casual dependence’, ‘path dependence’, or, ‘sensitivity to initial conditions’ that supposedly account for the modality of evolutionarily contingent forms (e.g. Beatty 2006; Desjardins 2011, 2016; Powell 2012; Sterelny 2005; Turner 2011). Certain biological forms are held to be contingent, or non-contingent, precisely because they are, or are not, at the end of a path dependent causal chain, for example. This inquiry into the relevant etiological structure for contingency is important because an advocate of the evolutionary contingency thesis (ECT) would assert that particular biological forms failed to robustly evolve because certain etiological conditions did not hold—e.g. the outcome was contingent because it was highly sensitive to initial conditions. However, aside from the question of which of the etiological structures best capture evolutionarily contingent dynamics, it is not clear *which biological forms* are meant to lack robustness and, furthermore, *how far robustness is to extend*—both of which makes conceptually grasping and empirically evaluating the thesis difficult. Despite the, now, frequent biological and philosophical discussions of the ECT, there has hitherto been no principled way of answering these two questions. Hence, there is a real need for some theoretical tools enabling one to fully spell out what the evolutionary contingency thesis amounts to. To this end, in “[The modal range](#)” section, I propose the idea of the *modal range* which allows contingency-theorists to relativise contingency claims to particular, more tractable, domains of interest.

The antithesis of the evolutionary contingency thesis—the robust view of life (RVL)—asserts (amongst other things) that certain biological forms are *robustly* realised which is to say that these forms are *repeatedly* realised across a number of evolutionary scenarios.<sup>1</sup> This view advocates that due to reasons of adaptive

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<sup>1</sup> As such, robustness is understood, precisely, in terms of a form’s repeatability. This is legitimate as robustness and repeatability are two sides of the same coin. In the philosophical literature, evolutionary contingency has primarily referred to the robustness of form (e.g. Sterelny 2005; Powell 2012) whilst, in the biological literature, it has often been about the repeatability of form (e.g. Vermeij 2006; Lenormand et al. 2009). Moreover, the more repeated a form is, the more robust the form is, and vice versa.

optimality or certain prevailing structural properties (sensu Sole and Goodwin 2001), certain forms are disposed to repeatedly evolve within *some* range of evolutionary scenarios. There is, however, a kind of phenomenon, seldomly investigated, that speaks against such repeatability. These are forms that, for one reason or another, have evolved *uniquely*. Often peculiar and distinctive, these forms constitute direct counter-examples to the robust view of life in that their evolution has been *singular* within the corresponding range. But their evidential role extends further than acting as mere counter-examples: the reasons for their singular evolution are informative of the way in which evolution has failed to be robust. Accordingly, one task of the present paper is to explicate what these reasons are and, more generally, investigate what these uniquely evolved forms—*evolutionary idiosyncrasies*—can say about the evolutionary contingency thesis.

Within the current evolutionary contingency literature, the bulk of the *empirical* evidence has been confined to ‘convergences’ which purportedly undermine the ECT by showing (i) that natural selection is ‘powerful’ enough to overcome historical encumbrances and, *a fortiori*, transcend individual phylogenetic constraints (e.g. Conway Morris 2003; Currie 2012a; Powell 2012) or (ii) that there are structural properties (or functional constraints) of evolutionary systems that rigidly circumscribe the space of possible or probable forms (e.g. Sole and Goodwin 2001; Salazar-Ciudad et al. 2003; McGhee 2011; Brandon and McShea 2010). The latter refers to physical, chemical, functional, dynamical, or other aspects of an evolutionary system that dispose evolution towards certain forms. For example, certain chemical facts true within some evolutionary system may bound evolution towards particular RNA configurations within that system. In contrast to convergences, evolutionary idiosyncrasies, as we shall see, do just the converse: they demonstrate that (i) history fails to be a limiting factor in the determination of form (within an evolutionary system) and/or that (ii) there are limited structuralities that circumscribe the space of possible or probable forms (within an evolutionary system).

The term ‘evolutionary idiosyncrasies’ is non-standard and was first introduced as the title of the third chapter of *Improbable Destinies* where Losos (2017) provides an impressive catalogue of various evolutionary *one-offs* from the duck-billed platypus to the Hawaiian Alula plant. The platypus possesses, amongst its suite of peculiar traits, a leathery, electro-sensitive bill conducive for prey-searching whilst the Alula plant embodies the odd appearance of voluminous flowers at the top of a long and thick stalk, leading to its being colloquially as ‘cabbage on a stick’. However, what makes idiosyncrasies evolutionarily interesting is not that they possess peculiar traits per se, but that their evolution has been a singular event. And, it is this singular evolution that I claim is at odds with the robust view of life and supportive of the ECT.

Despite the explicit intention of *Improbable Destinies* (Losos 2017) to evaluate the ECT, there is a noticeable paucity of investigation of the theoretical implications and/or philosophical significance of evolutionary idiosyncrasies *with respect to the ECT*. Nonetheless, Losos is to be commended for his pioneering step into a previously unrecognised area that is, as I argue in this paper, highly relevant for the ECT. Inspired by Losos’ lead, I consider possible explanations for the occurrence of

idiosyncrasies and conclude that there are, exhaustively, four non-mutually-exclusive explanations which threaten the repeatability of form in one way or another.

The first explanation—(i) *unique environments*—asserts that certain forms evolved only once because the environmental conditions and/or selective pressures leading to that form has been unique. Secondly, (ii) natural selection may have been *contingent or weak* such that natural selection responds differently to the same environmental conditions as to lack consistency in its production of form or, fails to repeatedly produce the *most superior form* for a given environment. Thirdly, there may be (iii) *multiple solutions to the same ecological problem* (also known as Functional Equivalence) such that there are several equally-as-adaptive solutions that can evolve by natural selection. Fourthly, (iv) *historicities*, or difference-making historical events with a low objective probability of occurrence, such as genetic drift events or migration events may apply diversionary tendencies across evolutionary scenarios such that the same form does not repeatedly arise. As I consider these explanations in greater depth, it will become clear that they each undermine, at least, one of two necessary premises of the robust view of life: what I call, environment-trait uniformity and environmental regularity. As such, observations of idiosyncrasies speak against a robust view of life and, *ipso facto*, are supportive of the ECT.

In addition, I shall formally characterise the positive evidential link between idiosyncrasies and the ECT in quantitative terms as to lay the groundwork for, subsequently, sketching a likelihood framework for evaluating the ECT in light of a given body of evidence consisting of a sequence of *opposing* data: the presence of idiosyncrasies *vis-à-vis* convergences. The need for the likelihood framework is motivated by the two common assertions that evolutionary contingency is a matter of ‘relative significance’ (e.g. Beatty 1995, 1997, 2006) and that evolutionary contingency can vary by degrees (e.g. Powell 2012). Both assertions allegedly present methodological issues for evaluating the evolutionary contingency thesis (Ibid.; Beatty 1995; Powell and Mariscal 2015); the former in systematically evaluating and balancing opposing evidence, and the latter in quantifying contingency’s exact degree of strength.

However, the likelihood framework proffered here kills two birds with one stone. It offers a powerful, objective means with which to evaluate between various ECT’s of different strengths, and to do so precisely on the basis of opposing evidence. The two hypotheses hitherto encountered—the ECT and RVL—can be understood as absolute extremes at the polar ends of a ‘contingency spectrum’ which contains a number of intermediary hypotheses. I submit that by way of a likelihood function, one can compute the probability of a body of evidence (i.e. some number of idiosyncrasies and convergences) conferred by any contingency hypothesis on the spectrum. In this way, the relative proportions of idiosyncrasies versus convergences can be informative of how evolutionarily contingent a particular domain is: the more idiosyncrasies there are *vis-à-vis* convergences, the more evolutionarily contingent the domain is. Hence, the methodological pessimism associated with evolutionary contingency varying in degree or being a ‘relative significance’ dispute can be dissolved.

The plan is as follows: I begin by introducing the crucial notion of the *modal range*, so that contingency claims can be made precise with respect to what it means

for a form to be robust or replicable. Following that, in “[Evolutionary idiosyncrasies and the Robust view of life](#)” section, I characterise evolutionary idiosyncrasies and illustrate the *prima facie* threat that they pose for the robust view of life. I, then, consider each of the four explanations for idiosyncrasies and explain how they each undermine the robust view of life. Moving on to the quantitative, in “[The likelihood framework and the contingency spectrum](#)” section, I advance two likelihood arguments (in the technical sense) to show that the likelihood ratio of idiosyncrasies in favour of the ECT (over the RVL) and the likelihood ratio of ‘convergences’ in favour of the RVL (over the ECT) are both above 1. Armed with these likelihood ratios which show the two phenomena’s direction of support on the contingency spectrum, I sketch a likelihood framework in which to evaluate the ECT given the idiosyncrasy-convergence dichotomy. In “[Evolutionary idiosyncrasies as differential evidence](#)” section, in order to demonstrate how idiosyncrasies can differ in their *evidential strength*, I consider certain statistical parameters, and draw a distinction between two different kinds of idiosyncrasies: *divergent idiosyncrasies* (DVI) and *disparate idiosyncrasies* (DPI), where the former is stronger evidence for the ECT than the latter. Moreover, both the evidential strength and the *evidential target* (i.e. which variant of the ECT) is also dependent on two conceptual *dimensions* in which idiosyncrasies can be defined and recognised. In this regard, I explain how an epistemic agent can adjust these dimensions to suit their respective epistemic projects.

## The modal range

Contingency claims assert varying levels of robustness or repeatability for certain biological forms across an array of evolutionary scenarios. But, barring some indeterminist exceptions,<sup>2</sup> most contingency-theorists advocate that questions of evolutionary contingency are about the prevalence of biological forms amidst the *variance* of certain, important evolutionary conditions of epistemic interest. In other words, a biological form is robust if it invariantly evolves in a wide range of evolutionary scenarios where (*inter alia*) the initial conditions, geographical space, developmental generators, history, or, even nomological laws (may) *differ* between scenarios.<sup>3</sup> Some of these differences may be counterfactual such that what is of concern includes non-actual possibilities—for example, would a particular biological form still evolve in face of certain facts contrary to the actual world? In fact,

<sup>2</sup> For example, Beatty (2016, 2017) thinks that no initial differences need to exist between alternative replays of the tape of life in order for there to be different biological outcomes. Differences will naturally accumulate over time between ‘replays’ in an indeterminist universe. Contingency questions, then, can even be about the prevalence of form amongst a series of initially identical evolutionary scenarios. (If, however, evolutionary scenarios are coarse-grained enough to contain ‘hidden variables’, then such a position need not oppose causal determinism).

<sup>3</sup> Naturally, some ranges set impossibly high standards for empirical evaluation. For example, it is difficult to determine the repeatability of forms in systems with nomologies inconsistent with the actual world, especially given that our empirical observations seem to inform only actual nomology. After all, our observations are privy to only the actual world. This pertains to the issue known as modal empiricism. Conversely, other ranges may be extremely narrow as to ask uninteresting questions.

contingency-theorists are often concerned with the evolution of forms in counterfactual scenarios (e.g. Beatty 1995; Conway Morris 2003; Beatty 2006; Powell 2012). As such, the range of scenarios need not be limited to the actual but can extend to the merely possible as well. For this reason, let us call the range of evolutionary scenarios under consideration for repeatability, the *modal range*.

The concept of the modal range is crucial in that it specifies the extent to which evolution is alleged to be contingent. To harken back to the introduction, it answers the question of how far robustness is to extend. A form is more-or-less robust within a *specifically-defined modal range* consisting of some evolutionary scenarios that may differ in certain respects. Contingency claims without a modal range index are not fully defined and are hence, difficult to conceptualise if not empirically evaluate. That is—contingency claims are defined in virtue of limiting the modal space (geographically, nomologically, historical, etc.) in which forms are alleged to be contingent. For example, if the modal range contains only evolutionary scenarios on Earth, then what is of concern is evolutionary contingency on Earth (e.g. Conway Morris 2003). Accordingly, then, for any question of evolutionary contingency, what is being asked is whether the evolutionary dynamics within some modal range are sufficient to result in the *repeated* evolution of certain forms within that range. A different modal range index entails a different contingency question and is likely to result in a different answer. In fact, the very same contingency-theorist (i.e. Vermeij 2006) may answer contingency questions in the affirmative for a modal range specifying early periods of life's history—i.e. *the Cambrian*—yet vehemently deny contingency for later periods of life due to the sentiment that certain phenomena including (but not limited to) phylogenetic inertia or generative entrenchment will heavily constrain downstream possibilities (c.f. Shanahan 2011; Wimsatt 2001).

In general, the determination of the modal range is dependent on the demands of a contingency-theorist's epistemic project. That is—if one were interested in the evolutionary contingency of some particular domain, then one ought to employ the appropriate modal range index as to track the relevant features of *that domain* and not of some other domain. Accordingly, given their respective epistemic goals, Conway Morris (2003) ought to consider the repeatability of forms within only evolutionary scenarios *on Earth* whilst Vermeij (2006) should take care to consider repeatability during the relevant *time periods*.

Nonetheless, due to the ambiguities afforded by a theoretically infinite number of modal range indices, one ought to be careful not to operationalise between two different senses of the ECT in any debate about the its truth, lest there be any argumentative cross-talk.<sup>4</sup> Moreover, when characterising a contingency-theorist's view, it is imperative to refer to the modal range at hand. Exegetically, Gould has often been mistakenly portrayed as *wholly* denying the repeatability of form (e.g. McGhee 2011, p. 271; see Powell and Mariscal (2015) for discussion). However, it is congruent with and, in fact, implied by Gould's larger view of life that there will be some repeatability of form due to frozen, developmental constraints (Gould 1977;

<sup>4</sup> There are, of course, some modal range indices that are 'nested' within other indices such that any disagreement may not necessarily be argumentative cross-talk.

Gould and Lewontin 1979). To this end, Gould even points to a case of repeatability (2002): the repeated evolution of feeding appendages in the crustaceans due to certain developmental precursors (also discussed in Powell and Mariscal (2015)). Importantly, Gould (1989) also claims that these developmental constraints could easily have been otherwise and hence, there is, undoubtedly, some contingency in this respect. The concept of the modal range allows one to recognise the nuances of Gould's view. That is—Gould can be understood as denying the contingency of evolutionary forms for modal ranges with deep developmental entrenchments yet asserting contingency for modal ranges without such developmental entrenchments (probably, modal ranges upstream in history).<sup>5</sup> I shall, now, characterise evolutionary idiosyncrasies and outline the threat that they pose for the RVL.

### Evolutionary idiosyncrasies and the robust view of life

To my knowledge, there has not yet been any formal definition of evolutionary idiosyncrasies (or equivalent<sup>6</sup>) in the biological or philosophical literature. Although evolutionary oddities and peculiar biological forms are often cited (usually, to convey a sense of awe), a lack of an explicit formulation of this class of phenomena in the literature is not entirely surprising given that, historically, little theoretical significance has been attributed to them. However, as I argue that the existence of uniquely evolved biological forms in nature has considerable bearing to the ECT, this class of phenomena has sufficient theoretical significance to merit explicit formulation:

**Evolutionary Idiosyncrasies:** biological forms that are *uniquely evolved* (within some modal range<sup>7</sup>)

As such, evolutionary idiosyncrasies are defined by their *singular evolution* and not by the form's uniqueness, per se. That is—there can be multiple instantiations of an idiosyncrasy: say, multiple platypus individuals, for example. The singular evolution of a form and its uniqueness are distinct notions and need not co-vary. Just as convergent evolution is defined by their having independent *bouts of evolution* rather than whether there are multiple instances of the form at hand, evolutionary idiosyncrasies (though uniquely evolved) can be multiply instantiated all the same. Conversely, if a form is unique, per se, in that it fails to be instantiated elsewhere in the modal range, it does not follow that the form is also an idiosyncrasy since

<sup>5</sup> Or to use Sterelny's (2005) term, Gould may be asserting 'conditional inevitability' whereby the condition is the developmental constraints: certain forms *necessarily* follow when those constraints are present.

<sup>6</sup> The closest, extant concepts are 'evolutionary novelties' and 'apomorphies' (c.f. Pigliucci 2008; Hennig 1966)—both of which do not capture a sense of *singularity* in a form's evolution.

<sup>7</sup> Like the ECT, evolutionary idiosyncrasies can also vary by being indexed to different modal ranges. However, what matters in considering their evidential import is whether this index (of time/space/possibility/etc.) is appropriate to capture an adequate sample size of alternative histories in order to infer certain propositions about the way evolution works. See ensuing discussion on the *scope of uniqueness*.

the form may have evolved multiple times but has been, subsequently, reduced to a single instantiation. All in all, what matters is whether a form has *independently evolved more than once* as to be informative of the evolutionary dynamics, relevant to contingency, of a domain.

But even then, a caveat is in order: there are two conceptual complications with defining and recognising evolutionary idiosyncrasies. The first pertains to *what it is* that is supposed to be uniquely evolved. In other words, what is the *subject of idiosyncrasy*? When it is said that a biological form<sup>8</sup> has uniquely evolved, is one referring to a *particular trait* like an electro-sensitive leathery bill, a *particular species* like the Hawaiian Alula, or, even a *particular biological population*? A clear denotation of the subject of idiosyncrasy is required before its evolution can be even precluded elsewhere.

Furthermore, the determination of the *subject of idiosyncrasy* may also be plagued by the so-called *grain issue*. Just as almost always encountered with convergence, whether two forms are alike or different depends on the grain of the form's description (Sterelny 2005; Currie 2012b; Powell 2012). For example, some coarse-grained traits like *predator avoidance* is so broad as to have, undoubtedly, evolved across several evolutionary lineages. Yet, at the same time, a finer-grained trait—say *camouflage*—is likely to be less ubiquitous. An even finer-grained trait like a *specific colour pattern* of camouflage would be even less common. In general, coarse-grained resolutions yield fewer idiosyncrasies than fine-grained resolutions, *ceteris paribus*. Consequently, the number of idiosyncrasies (or whether there are any idiosyncrasies at all) appear to be a matter arbitrarily dependent on grain specification.

But note that the determination of the subject of idiosyncrasy and the grain of analysis, though related, are distinct. It is just that determining the subject of idiosyncrasy will *involve* taking a stand on the level of grain to invoke. This is because possible subjects of idiosyncrasy (i.e. traits, species, populations, etc.) are often amenable to different descriptions due to differences in resolution. For example, the fastest animal on Earth, the peregrine falcon possesses many traits. There is the coarse-grained trait of 'being able to fly', a finer-grained trait of 'having wings', and, an even finer-grained trait of having 'pointed, stiff-feathered wings'. Yet, presumably, only the lattermost is a strong candidate for an idiosyncrasy. A different trait—say a pointed, *loose-feathered*- wing—is roughly at the same level of grain as the peregrine falcon's stiff-feathered wing, but it is clearly a *different* subject of idiosyncrasy which may or may not be uniquely evolved. However, settling on any one of these traits to be the subject of idiosyncrasy will, at the same time, answer the question of grain: for example, the trait of having 'pointed, stiff-feathered wings' will simply have a, fine-grained, description at that level. Graining is merely a property of a subject of an idiosyncrasy. The point is that insofar as a subject of idiosyncrasy has been determined, the grain of analysis will also be given. The election of the

<sup>8</sup> I mean 'form' in a very loose sense as to encompass almost any *biological outcome* of interest. As we shall see, this laissez-faire attitude is important for a contingency-theorist's framing of their epistemic project.



grain is important only insofar as it is part and parcel of specifying the subject of idiosyncrasy.

Secondly, there is the question of the *scope of uniqueness*. Forms are idiosyncratic if and only if they are uniquely evolved, but what does it take to be *uniquely evolved*? Let us say that Form A is uniquely evolved if and only if the same form has not evolved *elsewhere*. But, then, what does ‘elsewhere’ refer to? Are the forms to be considered ones found only on Earth or found beyond? Similarly, are forms in the ancient past or distant future to be considered? The widening of scope makes it less likely for any particular form to be uniquely evolved whilst narrowing the scope improves its chances.

These two complications present epistemic challenges in *defining and recognising* idiosyncrasies, but they do not undermine the concept, per se. That is—insofar as the subject of idiosyncrasy (including the grain of analysis), and the scope of uniqueness are specified, then there is very much a given number of idiosyncrasies in the world. For a ‘*theory of idiosyncrasies*’ then, it might be said that there are two *conceptual dimensions* in need of specification before idiosyncrasies are fully defined and thus, can be recognised. But the supposed conundrum is figuring out how, exactly, to specify these dimensions.

At this time, I respond briefly by pointing out that the specification of the subject of idiosyncrasy and the scope of uniqueness are wholly relative to the respective goals of individual epistemic agents and the nature of propositions they intend to make. This is because an alteration of either dimension will result in a shift of the *evidential target* of idiosyncrasies. For example, altering the scope of uniqueness shifts the variant of the ECT that is supported by idiosyncrasies since idiosyncrasies are now indicative of evolutionary singularity in a different modal range. That is—by altering the scope of uniqueness, idiosyncrasies are bouts of singular evolution *in face of a different set of variances* amongst evolutionary scenarios: perhaps, it is no longer singularity amongst scenarios with varying nomologies but varying histories. The independent variable(s) of the array has changed.

Recall that it is crucial in any debate about the contingency of evolution for the participants to hold fixed the modal range in which evolution is alleged to be contingent, lest there be argumentative cross-talk. So, suppose a contingency-theorist was interested in the evolutionary contingency of the terrestrial domain (i.e. on Earth). In this case, idiosyncrasies are evidentially relevant *only if* they are informative of the evolutionary dynamics *of that domain*. Any different—say if the scope of uniqueness of idiosyncrasies was extended to only one continent—then idiosyncrasies fail to be informative of the evolutionary dynamics (e.g. the power of natural selection or the existence of certain structuralities) present on Earth (barring extrapolation from continent to planet). As such, idiosyncrasies would not tell us about the wholesale repeatability of form on Earth, but only on one continent. Accordingly, if one were interested in the power of natural selection on Earth, then an Earth-wide scope of uniqueness would be appropriate. In other words, it is epistemically imperative that the scope of uniqueness of idiosyncrasies *correspond* to the modal range of the ECT variant in question. In a return to the topic of *differential evidence* in “[Evolutionary idiosyncrasies as differential evidence](#)” section, we shall see that an alteration of the subject of idiosyncrasy also shifts the evidential target. In general,

taking a position on either of the two dimensions will not only affect the number of idiosyncrasies recognised but alter their evidential implications as well. Hence, the specification of the two conceptual dimensions depends on the epistemic demands of a contingency-theorist's project.

In *Improbable Destinies*, Losos (2017) offers many examples of idiosyncrasies but, perhaps, most notable is the semi-aquatic *duck-billed platypus*, found only in eastern Australia. The platypus' unique evolution is exemplified by the amalgamation of several peculiar features: its mammalian egg-laying, venomous spur, leathery bill, and prey-sensing electroreceptors. Losos' point is that, *as a whole*, there has been no other species like the platypus.<sup>9</sup>

There is tension between such cases of evolutionary idiosyncrasies and the robust view of life: if biological forms were *robust* in their evolution, then it would be striking that idiosyncratic forms like that of the platypus did not evolve more than once. This is because the robust view of life stipulates that the same evolutionary outcomes will *repeatedly* evolve within some modal range whilst idiosyncrasies assert, precisely, that there has been *singular* evolution within that modal range. *Ceterus paribus*, these are contradictory assertions.

The source of the tension stems from the fact that the robust view of life explains, in part, such repeatability by appealing to there being certain, definite *environment-trait dyads*: given any one environment, there is *necessarily* a given trait.<sup>10</sup> In other words, the robust view of life requires that certain evolutionary conditions *necessarily* lead to particular evolutionary outcomes.<sup>11</sup> This is either manifested by (i) a *Hard Adaptationist* sense of natural selection (Amundson 1994) that dictates that certain environmental pressures are met with the most superior solution (e.g. McGhee 2011; Powell 2012), or, (ii) that non-selective nomological aspects or the so-called *structuralities* of the environment dispose one particular outcome (e.g. McShea 1994; Sole and Goodwin 2001; Stayton 2008; Brandon and McShea 2010). But this *environment-trait uniformity* alone is not enough for robust repeatability since it is possible for same evolutionary conditions to fail to repeatedly exist within the modal range.

<sup>9</sup> Depending on the scope of uniqueness, the platypus may be an inapt example of an evolutionary idiosyncrasy as there are closely-related and similar, albeit extinct, species such as the *Obdurodon* or *Ornithorhynchus*. Perhaps, it was the common ancestor to these three species that was the idiosyncrasy. Nonetheless, regardless of any difficulty in pinpointing idiosyncrasies, the conceptual point for their significance still stands.

<sup>10</sup> As a note aside, it is, sometimes, tricky to define the environment-trait dyad. As per Brandon (1990), environments are always relative to an organism. So, whilst two organisms *may* seem to occupy the same environment, they may nonetheless be exposed to subtle differences in environmental pressures. Thanks to an anonymous referee for this reminder.

<sup>11</sup> Historically, this idea has had strong support by evolutionary biologists due, in part, to a battery of statistical tests confirming significant correlation between environment and phenotype for individual taxons (e.g. Gittleman 1981; Felsenstein 1985; Felsenstein 2004; Hansen et al. 2008). However, Kluge (2005) argues that little can be inferred from this correlation. The correlation has also been met with much push-back from claims cautioning an overshoot of its implications (e.g. environment-trait correlation does not show adaptationism), stemming from the 'internalists' and the like.

Accordingly, the remaining half of the explanation for robust repeatability is that there is, in fact, *environmental regularity* such that there are multiple instances of the same evolutionary environment within the modal range.<sup>12</sup> Putting these two parts together, the robust view of life says that a form,  $F_1$ , is repeatedly realised in some modal range (say, within all Earth-like planets in the universe at all times) because (i) environment  $E_1$  necessarily gives rise to form  $F_1$  due to some evolutionary force (e.g. selection or drift), *and* (ii) environment  $E_1$  can be widely found on Earth-like planets in the universe. Environment-trait uniformity and environmental regularity are two necessary premises (amongst others) that are required of the robust view of life in order to assert the repeatability of form. If, for instance, there was no environmental regularity within the modal range concerned then, despite the power of natural selection or functional constraints to dispose forms in certain environments, there would nonetheless be no repetition of form.<sup>13</sup> Alternatively, if certain environments do not guarantee particular forms, then despite an abundance of similar environments, the same form need not repeatedly result.

Accordingly, at a more fundamental level of analysis, the tension exists because observations of idiosyncrasies threaten the truth of the two premises of a robust view of life. That is—observations of idiosyncrasies provide reasons to dissolve the classical environment-trait dyad or reject that there are alternative histories with similar evolutionary conditions within the modal range. This is because the individual *explanations* for idiosyncrasies, themselves, logically contradict environment-trait uniformity and/or environmental regularity. To see this, let us now consider the four explanations in turn.

## Explanations for evolutionary idiosyncrasies

### Unique environments

One obvious explanation for occurrences of idiosyncrasies is that the *evolutionary environment* in which an idiosyncrasy evolved was unique and so, it was no surprise that the idiosyncrasy evolved only once. In other words, the set of conditions that led to the evolution of an idiosyncrasy failed to be present elsewhere (within the modal range) such that the form, supposedly guaranteed by the environment, did not evolve elsewhere (within the modal range). Since an evolutionary environment (*sensu lato*<sup>14</sup>) may be manifested by the set of selective pressures or non-selective

<sup>12</sup> Millstein (2000) has made the point that even in the face of natural selection, the macroevolutionary pattern will be stochastic if lineages were driven by a wide array of selective pressures that are unrelated or, at least, random with respect to each other. Brandon and McShea (2010) made a similar point.

<sup>13</sup> Logically, there is one exception whereby the same form can answer many environmental demands. This is the converse of the multiple solutions to the same ecological problem and *may be* exhibited by phenomena such as ‘environmental plasticity’. However, as we shall see, if the MST is true, then this exception cannot apply.

<sup>14</sup> The sense of ‘evolutionary environments’ vary widely in the philosophical and biological literature. My operationalisation of it here is in contrast to, for example, Losos’ (2011) more restrictive sense where

nomological properties (i.e. structuralities *sensu* Sole & Goodwin), this could mean that the selective pressures were unique such that natural selection did not yield a similar form elsewhere or that the structuralities of the environment were unique such that a similar form did not result elsewhere.<sup>15</sup> (Or even that the amalgamation of both selective pressures and structuralities were unique.) In essence, a unique environment presents evolutionary conditions, not found elsewhere within the modal range, with which evolutionary forces are to operate. And so, it is no surprise that the result of these forces is a form that evolved only once within the modal range. Returning to the platypus example, perhaps, its evolution was one-off *because* the environmental conditions conducive to its evolution failed to be present elsewhere.

All in all, unique environments suffice to explain the occurrence of idiosyncrasies, but the existence of unique environments is logically opposed to the environmental regularity premise of the robust view of life. For obvious reasons, there cannot be both environmental regularity (i.e. more than one instance of the same environment) and a unique environment within a modal range. And so, if unique environments are to explain the occurrence of an idiosyncrasy within a modal range, then the robust view of life is false for that modal range.

Empirically, this sort of explanation is compelling. A recent review paper by Stuart et al. (2017) points out that deviations from the expectation of ‘convergences’ is often a result of subtle environmental heterogeneity or subtle differences between environments. Other studies have a similar conclusion (e.g. Landry et al. 2007; Matthews et al. 2010; Moore et al. 2016). But this is not the only explanation for occurrences of idiosyncrasies.

### Weak or contingent natural selection

Given that the natural habitat of the platypus (e.g. streams and ponds) appears to be ubiquitous on Earth (Losos 2017, p. 88), Losos wonders why forms similar to the platypus could not be found elsewhere other than eastern Australia. In other words, for Losos, the evolutionary environment for the platypus is clearly not unique. His first gesture at resolving this curiosity is to point to the possibility that natural selection could be limited in its ability to generate the same form. That is—either natural selection is weak or contingent (he uses the word “unpredictable” in lieu of contingent<sup>16</sup>). If natural selection were weak in the sense that it does not always succeed

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Footnote 14 (continued)

an evolutionary environment comprises solely of selective pressures *without inclusion of any structuralities*.

<sup>15</sup> As we know from Lewontin (1983), organisms are often part of the environment and can *constitute* as selective pressures in an environment. Thus, an environment may be unique or fail to be unique because of the constellation of biotic creatures present. So, the phenomenon of *competitive exclusion* can be subsumed under the explanation of unique environments: a form did not repeatedly evolve (in an initially unique environment) because a similar form has already taken its place, thereby changing the selective environment.

<sup>16</sup> Exegetically, it does not appear that Losos refers to ‘unpredictability’ in the epistemic sense. In order to avoid conflation with a distinct, epistemological notion about what one can know about natural selec-

in resulting in the *most superior* solution, then identical evolutionary environments need not result in the same biological form under natural selection's crank. For the advocate of the robust view of life, optimality reasons can explain why certain forms are robust (i.e. forms are robust *because* they are adaptive peaks) but such reasons must be coupled by some mechanism (i.e. hill climbing mechanism) that sufficiently ensures the evolution of the superior trait. Without the latter—if *natural selection were 'weak'*—then there is no reason to think that a trait will be robustly realised even if the trait in question were most superior.

As for Losos' claim that idiosyncrasies can be explained by natural selection that is 'contingent', it is not clear what is exactly meant by this though one may surmise given his reference to random mutation and mutational order. Perhaps, natural selection is contingent in that natural selection is dependent on low probability events (often referred to as 'chancy' or 'stochastic' events) that generate the suite of genetic material made available and their *ordering*, like random mutation and mutational ordering (Mani and Clarke 1990), respectively. But if natural selection is contingent in this sense, then natural selection cannot guarantee a particular outcome given certain evolutionary environments; different outcomes may result depending on chancy precedents.

Accordingly, idiosyncrasies can occur despite any environmental regularity because natural selection failed to guarantee environment-trait uniformity due to either (i) selection's limited ability to produce the most superior form or (ii) the chancy availability of genetic variance with which selection is dependent upon. Either way, an explanation of idiosyncrasy invoking weak or contingent natural selection dissolves the environment-trait dyad since certain evolutionary environments fail to guarantee particular outcomes.

But notice that explanations invoking the weakness or contingency of natural selection nonetheless ultimately rely on historical events. As above, natural selection is weak only because it is at the mercy of past phylogenetic constraints and other historicities (c.f. Gould and Lewontin 1979). Likewise, natural selection is contingent only because it is dependent on the occurrence of prior historical events (e.g. random mutation) that supposedly lack counterfactual robustness. But this is no cause for concern for, as we shall see, the various explanations for idiosyncrasies are not mutually-exclusive and may work in tandem to undermine the RVL.

Furthermore, if what is meant by natural selection being contingent is that it fails to guarantee a particular outcome given certain environmental conditions, then there appears to be yet another way in which natural selection is contingent. This is because certain environmental conditions may leave open a choice of equally-as-effective design solutions (Arnold 1983; Beatty 2008). That is—on the basis of adaptive value alone, the solutions may be more-or-less indistinguishable from one another. Thus, natural selection cannot possibly favour one solution over another (whichever solution is reached must be due to non-adaptive factors). There may be

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Footnote 16 (continued)

tion, I shall take Losos as referring to the 'contingency' of natural selection in its ability to yield robust forms.

multiple (equally adaptive) solutions to the same ecological problem—let us call this the Multiply Soluble Thesis (MST).

### Multiple solutions to the same ecological problem

Darwin brushed past this very idea in considering the range of the orchid's fertilisation mechanisms (1862). He noted that orchid fertilisation was facilitated by insects, but such a mechanism was, in principle, liable to lead to inbreeding which would incur substantial adverse fitness effects over time (Ibid.)—modern studies confirm this (e.g. Smithson 2006). At the same time, theoretical considerations stipulate that orchid fitness would increase by maximising reproduction. Thus, orchid fertilisation may be said to have (at least) two primary ecological problems: the maximisation of reproduction by cross-pollination and the avoidance of inbreeding.

But Darwin further noted that the various species of orchids were, for all intents and purposes, subjected to identical environments since they were open to visitation by the very same complement of insect species.<sup>17</sup> Yet orchids showed substantial diversity in their morphology in enlisting insects for cross-pollination. In the case of the *Orchis mascula*, there are two adhesive sacs of pollen masses suspended by thin elastic threads. The nectary of the *Orchis mascula* was in such a way that when an insect attempts to feed, it would undoubtedly brush past these sacs of pollen, thereby attaching the sacs to themselves, and, subsequently, bring pollen to its next destination (another *Orchis mascula*, perhaps). The *Catasetum saccatum*, on the other hand, violently launches pollen sacs downwards at insects when certain, elaborate triggers are activated. The point is that orchids exhibited multiple solutions to the same ecological problems.<sup>18</sup> In the modern ecological literature, this has been come to be known as the many-to-one mapping of form to function (e.g. Alfaro et al. 2004; Wainright et al. 2005; Thompson et al. 2017).

Losos too recognizes the idea of the MST and considers it as a candidate explanation for idiosyncrasies and, in particular, the unique evolution of the platypus. Although the environmental conditions in eastern Australia that gave rise to the platypus may be present elsewhere on Earth, the range of solutions may ultimately be underdetermined by the environmental conditions. That is—perhaps, other species with morphology distinct from the platypus could answer the same ecological demands to that of the platypus. And hence, the same form need not repeatedly evolve in the same environments. In this way, the environment-trait dyad is once again broken such that particular outcomes are no longer guaranteed by certain

<sup>17</sup> Of course, Darwin may have been operating with a coarse-grained 19th century lens here. But this does not take away from the example's point.

<sup>18</sup> Perhaps, Darwin's lens might have been too coarse, after all. Finer-grained lenses might lead one to think that the ecological problems encountered by the *Orchis mascula* and *Catasetum saccatum* are not the same. Since the two species must evolve a means of avoiding inbreeding, they might do well to evolve different morphology as to *specialise* in different insect species. The salient question for whether orchids do, in fact, share the same ecological problems is: are the different orchid species truly visited by the *same* complement of insects?

environments. Idiosyncrasies that are explained by the MST are opposed to the robust view of life in virtue of undermining environment-trait uniformity.

In demonstrating the MST, there are a host of empirical cases that document significant morphological diversity for the *same* function. For instance, Young et al. (2009) studied how a many-to-one mapping of form to function can lead to morphological diversity in shrews generating the same amount of jaw force. Similarly, the canonical stickleback studies (e.g. Wainright et al. 2005; Thompson et al. 2017) illustrate that the MST can apply selectively to feeding structures. These studies agree that the lower jaw structure of the threespine stickleback has exhibited a strong *linear relationship* with its function (i.e. lever ratio) or a *one-to-one mapping of form to function*. In other words, the MST is false for the lower jaw structure. However, two other structures of the threespine stickleback, the epaxial-buccal cavity and 4-bar structure show significant functional equivalence in their respective functions (as measured by ‘suction index’ or ‘kinematic transmission’). Thompson et al. (2017) further demonstrated that *because* of a many-to-one mapping of form to function, there was less *repeated evolution* of the latter two structures.<sup>19</sup> Putting aside methodological and grain issues, these studies extend plausibility to the MST.

## Historicities

It is true that an explanation for idiosyncrasies based on the MST undermines the robust view of life by dissolving the environment-trait dyad. However, logically-speaking, the MST per se is not enough to entail the unique evolution of a form. Just as there is no positive reason to think that any one particular form will repeatedly evolve when there are equally adaptive alternatives (in design space), there is no positive reason to think that a different solution will arise at every evolutionary bout even when there are alternatives. Rather, there must be some reason for why it is that the same design solution was not elected even in the presence of alternatives.

This brings us to the fourth explanation for idiosyncrasies: difference-making historical events with low objective chance of occurrence. Let us call this *historicities*.<sup>20</sup> Even if there were several equally-adaptive solutions to the same ecological problem, whichever form natural selection or genetic drift produces depend upon certain preceding historical events like random mutations or their ordering. For example, if the necessary complement of genetic variation for the evolution of wings did not arise through random mutation then there can be no such evolution of wings. In this way, low probability historical events such as historicities limit the directionality of an evolutionary population’s movement through adaptive space. Alternatively, historical factors may place an evolutionary population initially closer to one peak than another and thereby, increasing its probability of climbing the closer peak.

Historicities relevant to the ECT encompass many phenomena and can be biological or non-biological. Biological historicities include (*inter alia*) random mutation,

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<sup>19</sup> Their study used the term ‘parallelism’ but their definition did not have encompass a developmental component. So, for consistency, I take it they meant ‘repeated evolution’ or ‘convergence’, more broadly.

<sup>20</sup> I follow Desjardins’ terminology (2016).

mutational order, migration events, and phylogenetic constraints due to ancestry. Certain migration events with low objective chance of occurrence such as ones prompted by volcanic eruption may result in gene flow into a population with significant outcome difference making effects. In this regard, the empirical literature has demonstrated that differential gene flow due to differential migration resulted in significant phenotypic divergences of the lake-stream stickleback (Hendry and Taylor 2004) and, indeed, other organisms (Hendry 2017).

Famously due to Gould (1989), one commonly discussed historicity in the contingency literature has been historical events that severely circumscribe downstream outcomes via the generation of phylogenetic constraints. Indeed, one principal argument in *Wonderful Life* (1989) was that the survivors of Cambrian extinction *could have easily been otherwise* such that the phylogenetic constraints (e.g. *bauplan*) of our vertebrate clade, which descended from the reigning survivors of a supposedly indeterminate sampling event (i.e. Cambrian Extinction), had a low objective probability of occurrence. According to Gould (Ibid.), extant vertebrates could easily have had different body plans and hence, be markedly different. The thrust of this argument comes from the *low objective probabilities* of the survival events during the Cambrian such that replaying the Cambrian period would undoubtedly or, more accurately, *probably* result in a different surviving menagerie. In general, on account of the low probability of phylogenetic events, evolutionary systems within a modal range are probable to have different phylogenetic constraints. This is because it is, by definition, relatively improbable for the same low probability phylogenetic event to occur in more than one evolutionary system. Thus, there is a probabilistic expectation that different evolutionary systems are to have different phylogenetic constraints. And, for this reason, idiosyncrasies may result since the form is improbable to evolve again in alternative evolutionary systems.

Non-biological events include (*inter alia*) asteroid impacts, global climate change, and certain perturbations stemming from outside the evolutionary system. Despite their non-biological nature, the key is that these historical events are difference-making to the *evolutionary outcome* and have a low objective probability of occurrence—e.g. they are ‘chancy’, ‘stochastic’, or ‘random’. Without the latter, it is possible for the same historical events to occur ubiquitously within a modal range as for the same forms to repeatedly evolve.

An explanation of idiosyncrasies founded in historicities can undermine the environment-trait uniformity premise of the robust view of life through its interaction with natural selection: an environment fails to guarantee a specific form because certain historicities such as random mutation limited natural selection. Alternatively, the environmental regularity premise can be undermined by historicities, such as asteroid impacts or volcanic eruptions, that occur in some but not all environments, thereby introducing differences amongst environments in a modal range. That is—historicities may, sometimes, produce unique environments within a modal range (though they need not<sup>21</sup>). In the former case, natural selection is limited in virtue of

<sup>21</sup> Historicities and unique environments are distinct concepts although they often come hand-in-hand (they are not mutually-exclusive, after all). As already mentioned, historicities can constitute as chance events in migration or extinction resulting in differential genetic availability and, subsequently, idiosyncrasies, without ever producing a unique environment.



historicalities (i.e. mutation events) whilst in the latter, an environment is unique due to historicalities (i.e. asteroid impact or volcanic eruption).

Having considered the four explanations for idiosyncrasies, it is helpful to consider their effects in terms of Simpson's (1944) adaptive landscape metaphor (not to be confused with Wright's earlier adaptive landscape of *gene frequencies*). Recall that the MST asserts that there are multiple equally-as-adaptive solutions to the same environmental problem. This can be understood as the prevalence of several equally-as-high peaks on the adaptive landscape.<sup>22</sup> So, one explanation for the occurrence of idiosyncrasies is that there were several adaptive peaks, each encompassing a distinct solution, on the landscape.

However, whichever peak is sought can highly depend on historical factors: either those that determined the starting conditions on the adaptive landscape or those that influence the directionality of movement (e.g. the generation of genetic variation upon which natural selection can act) across the adaptive landscape. On the adaptive landscape, if natural selection is, indeed, weak or contingent, then there is a limitation in the directionality of movement across the topographical space. In other words, the supposed hill-climbing mechanism is limited. But again, such a limitation would be ultimately due to historical events such as random mutation or drift events.

Lastly, the topography of an adaptive landscape is, itself, a manifestation of the environment. That is—the ridges and contours are determined by the environmental conditions. Hence, unique topographies correspond to unique environments. A unique environment can, then, be understood to provide a unique topography on which evolutionary forces act. All in all, the adaptive landscape metaphor is meant to emphasise that the four explanations for idiosyncrasies are not mutually-exclusive and may, sometimes, work in tandem to explain particular bouts of idiosyncrasies: even if there are many peaks, whichever adaptive solution is sought can depend on the details of natural selection and/or historical factors. Likewise, the determination of the topography (i.e. environment), itself, is sometimes dependent on the historicalities.

## The likelihood framework and the contingency spectrum

Thus far, I have argued that each of the four explanations of idiosyncrasies undermine at least one of two necessary premises for the robust view of life and, as such, idiosyncrasies are evidence against the robust view of life. Moreover, since the RVL and ECT are contradictory views, evolutionary idiosyncrasies also serve as evidence for the ECT. But how might we invoke idiosyncrasies as evidence in further analyses?

In this section, I sketch a likelihood framework in which to evaluate contingency hypotheses in light of a body of evidence. More specifically, I model the

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<sup>22</sup> Notice that as the number of equally-as-high peaks reaches infinity, it is akin to the adaptive landscape being absolutely 'flat' whereby genetic drift would completely take over.

idiosyncrasy-convergence dichotomy as Bernoulli processes and I define a *likelihood function* that will yield, from a given a set of data (i.e. observations of idiosyncrasies vis-à-vis convergences), a likelihood distribution for all of the hypotheses on the ‘contingency spectrum’. In other words, for any given set of observations consisting of some number of idiosyncrasies and some number of convergences, one can compute the *likelihood* (in the technical sense) of various hypotheses that differ in the degree of contingency that they assert. Subsequently, one can also determine which hypothesis has the maximum likelihood (via maximum likelihood estimation methods<sup>23</sup>). That is—even if a number of contingency hypotheses is *consistent* with the data, there will nonetheless be *one* hypothesis that confers the greatest probability on the data. And, according to the Law of Likelihood (see later), this hypothesis is one that is best evidentially supported by the data.

For the proponents of Bayesianism, one can further derive the posterior probability mass function (pmf) by applying this likelihood function to some appropriate prior distribution. Quite powerfully, this would, then, yield the conditional probability of any ECT hypothesis in light of the evidence; however, this Bayesian inference would nonetheless be severely limited by the determination of the priors (where uniformity *may not* be appropriate) and the quality/quantity of the data.<sup>24</sup> Regardless, the merit of the likelihood function stands on its own and is found in the function’s ability to produce different likelihoods for a range of hypotheses that correspondingly differ in their assertion of the degree of contingency for some modal range or domain.

Evolutionary contingency is said to vary in degrees (e.g. Beatty 1995, 2006; Powell 2012; Turner 2011). By that, it is meant that different domains may exhibit different levels of evolutionary contingency; there may be some domains where contingency reigns strongly whilst there may be other domains where robustness is the norm. In domains where contingency is strong, biological forms are less repeatable or less robust than in domains where contingency is weak. Accordingly, I submit that we can understand the RVL and ECT as extremes on the polar ends of a contingency spectrum with an infinite number of intermediary hypothesis in the middle (see Fig. 1).

Recall that the ECT denies that there is *any* repeatability within a modal range such that all forms within that range are idiosyncrasies. Conversely, the RVL says that there *is* repeatability and that there are no idiosyncrasies at all. Both of these hypotheses are radical in the degree of contingency they assert and no actual contingency-theorist advocates either of them. Rather, the more plausible hypotheses lie in the intermediate, and it is just that contingency-theorists disagree on which of the intermediary hypotheses is true. As mentioned, fortunately, likelihood functions provide a means of evaluating between the various hypotheses on the spectrum—or, in other words, evaluating the strength of contingency—given some appropriate

<sup>23</sup> In this case, there is (fortunately) a closed-form analytic solution available since I am modelling the ‘contingency trials’ as Bernoulli processes: e.g. # of idiosyncrasies/total observations.

<sup>24</sup> There is a litany of papers on this issue across various disciplines. So, I shall not rehearse the points here. See Howson and Urbach (1989) for what I take to be the definitive guide on Bayesianism.

data. But what is considered appropriate data, and, furthermore, what would the data be supportive of?

The previous section showed that evolutionary idiosyncrasies are evidence against the RVL and are evidence *for* the ECT. It seems that idiosyncrasies point towards the ECT. However, there is a different kind of observation that seems to point in exactly the opposite direction. These are observations of ‘convergences’ which have had much discussion in the contingency literature. Roughly put, *convergences* are the repeated evolution of the same form from *sufficiently independent* taxa/species/lineages/starting points.<sup>25</sup> I shall reconstruct these points in probabilistic terms as to adhere with the likelihood framework. I do this by advancing two *likelihood arguments* to show that ‘idiosyncrasies’ evidentially favour the ECT (over the RVL), and ‘convergences’ evidentially favour the RVL (over the ECT). In other words, I shall show that (i) the probability of idiosyncrasies given the ECT is higher than the probability of idiosyncrasies given the robust view of life, and (ii) the probability of convergences given the RVL is higher than the probability of convergences given the ECT.

The first argument can be depicted in the terms of comparative likelihoods, where ‘IDIO’ refers to observations of evolutionary idiosyncrasies and ‘RVL’ refers to the robust view of life:

$$(IE1) \Pr(\text{IDIO} \mid \text{ECT}) > \Pr(\text{IDIO} \mid \text{RVL})$$

If the left-hand term is greater than the right-hand term, then the likelihood ratio in favour of the ECT is above 1. Then, according to Hacking’s (1965) ‘Law of Likelihood’ or, in the form more common today (i.e. Sober 2008), *observations of idiosyncrasies count as evidence for the ECT (over the RVL)*:

**Law of Likelihood**<sup>26</sup>: An observation O evidentially supports (is in favour of)  $H_1$  over  $H_2$  if and only if  $\Pr(O \mid H_1) > \Pr(O \mid H_2)$  (Sober 2008)

Evolutionary idiosyncrasies, as defined, are biological forms that have uniquely evolved such that they have not evolved elsewhere within the modal range. If the ECT were true of some modal range such that there is little or no repeatability within that range, it would not be a surprise that there are idiosyncrasies within that modal range. However, if the RVL were true such that there is much repeatability, then the existence of idiosyncrasies which, by definition, defy repeatability would be a surprise. Therefore, (IE1) is true, and idiosyncrasies favour the ECT over the RVL.

<sup>25</sup> There are numerous discussions on what it takes to be sufficiently independent. See Currie (2012b), Powell (2012), Powell and Mariscal (2014), and Pearce (2012). Of considerable importance is the ‘parallelism-convergence distinction’ that alleges that some commonly cited instances of ‘convergences’ are actually instances of parallel evolution which fail to inform the contingency debate on account of their superficial independence. Rather, ‘genuine convergent evolution’ ought to be our evidence (Powell 2012; Powell and Mariscal 2014).

<sup>26</sup> According to Sober (2008), this law also offers a “quantitative element” (Ibid.) that allows one to infer the *degree of support* O can offer  $H_1$  over  $H_2$ . But this is extraneous to our current concerns here, especially given our present inability to quantify, exactly, the likelihoods. We can recognize only their directions of inequality.

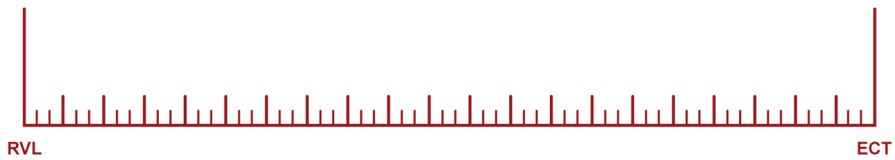


Fig. 1 Contingency spectrum

On the other hand, convergences or the independent origination of the same form would not be a surprise if the RVL were true. This is because the RVL stipulates that there are cases of repeated evolution of the same form within a modal range. However, if the ECT were true such that there was little or no repetition of form, then one would not expect convergences. So, IE2 is also true such that convergences favour the RVL over the ECT:

$$(IE2) \Pr(\text{CONV} \mid \text{RVL}) > \Pr(\text{CONV} \mid \text{ECT}) \text{ [‘CONV’ refers to convergences]}$$

It is now clear which ends of the contingency spectrum, these two phenomena point towards. Observations of idiosyncrasies push us towards the right of the contingency spectrum (viz. towards the ECT), and observations of convergences should push us towards the left of the contingency spectrum (viz. towards the RVL).<sup>27</sup> Now, suppose that one were interested in the degree of contingency (and, *a fortiori*, the truth of contingency) in some domain, and had observed some number of idiosyncrasies and some number of convergences. In this case, one might ask for the *comparative evidential support*, by the data observed, for all of the hypotheses on the contingency spectrum. And, to answer this question, one would need to compute the *likelihood* of every hypothesis given the data (implicit, here, is the Law of Likelihood). This can be done by way of a likelihood function. Furthermore, one might wish also to determine which hypothesis has the *greatest likelihood* in which case there exists maximum likelihood estimation (MLE) methods. The thesis with the greatest likelihood is the one best supported by the evidence.

A simple likelihood function can be, without difficulty, defined under certain idealised conditions and assumptions.<sup>28</sup> Firstly, both observations of idiosyncrasies

<sup>27</sup> Due to the assumption of Evidential Weight, it is assumed that they the two observations push in opposite directions by the *same amount*. See trailing discussion.

<sup>28</sup> This is not to say that a likelihood function cannot be produced given unideal conditions. For example, even if individual observations were not mutually independent, one can just tediously calculate the joint probability of  $(x_1, \dots, x_{(n)} \mid \theta)$  instead of individual terms  $P(x^i \mid \theta)$ . Secondly, observations of idiosyncrasies and convergences are assumed to be one-dimensional here. If they are not, then we can code our observations according to d-dimensions. Thirdly, observations are taken to be binary in that they are either idiosyncratic or convergent, but it is sometimes suggested that convergences are spectral (Hall 2007). If the real-world observations are not binary, then we can model using other distribution models such as a Gaussian instead of a Binomial distribution and employ probability density functions instead of probability mass functions. This allows us to differentiate between different degrees of idiosyncrasies and convergences. Regardless, there currently exists no good *graded* account of convergences and/or idiosyncrasies. All in all, in my binomial model here, I am assuming an idiosyncrasy-convergence dichotomy. If this assumption is false, then it is just that a different model would be appropriate.

and convergences must occur within the *same modal range*. After all, evidence for or against contingency in some domain is irrelevant for evaluation of the ECT in another domain. Secondly, observations of idiosyncrasies and convergences must be commensurable. By this, I take it that, at least, idiosyncrasies and convergences must be specified at the same level of analysis and to the same scope of uniqueness. Recognising the convergence of coarse-grained trait like agricultural farming hardly counts against an idiosyncrasy about specific mechanisms of feeding structures. Thirdly, we might want to *assume* (for arithmetic simplicity, though we need not<sup>29</sup>) that idiosyncrasies and convergences have the same ‘evidential weight’ such that one observation of idiosyncrasies counts exactly against one instance of convergences, and vice versa. That is—the difference in likelihoods of the ECT and the RVL given idiosyncrasies, and the difference in likelihoods of the RVL and ECT are identical<sup>30</sup>:

$$\text{(Evidential Weight) Pr (IDIO | ECT) - Pr (IDIO | RVL) = Pr (CONV | RVL) - Pr (CONV | ECT)}$$

If Evidential Weight is true, then the ECT will raise the probability of any instance of idiosyncrasies by just the same amount as the RVL will raise the probability of any instance of convergences. In other words, idiosyncrasies and convergences push towards opposite sides by, exactly, the same amount. Fourthly, we assume mutual independence between all the observations. If these four conditions hold, then a binomial likelihood function can be defined to yield a likelihood distribution. Let us define this likelihood function by way of example.

Suppose that some researchers were interested in the evolutionary contingency of the South American continent. They make a total of 100 observations that consists of 64 idiosyncrasies and 36 convergences. If we understand the sequence of idiosyncrasies and convergences as a sequence of binary events, then modelling the data as a *binomial distribution* is appropriate since the observations are independent Bernoulli processes. Let the sequence of events serving as our data be:  $x_i = \{x_1, \dots, X_{(n)}\}$ , whereby an idiosyncrasy is denoted by 1 and a convergence is denoted by 0. In our sample, the sequence might thus be coded as ‘1, 1, 0, 1, 0, ... n’ such that total of 1’s is 64 and total of 0’s is 36. (Of course, there are many sequences in which the data contains 64 idiosyncrasies and 36 convergences; this is accounted for by the binomial coefficient of ‘n choose x’). The likelihood function for a *binomial distribution* is given by:

<sup>29</sup> The likelihood framework does not depend on the truth of this assumption. If the assumption were false such that observations of convergences and idiosyncrasies are weighted differently, then we would merely need to incorporate the right weighting. To this end, we can denote a ‘weighting ratio’ of idiosyncrasies versus convergences as  $LD_i/LD_c = y$ . If  $y = 1$ , then the weightings of idiosyncrasies and convergences are the same (and Evidential Weight is true). If  $y < 1$ , then convergences are weighted heavier than idiosyncrasies. Accordingly, we can additionally take the product of  $y$  and the ratio of  $\frac{x}{n}$  to arrive at the  $\theta$  with the maximum likelihood as to incorporate uneven weighting. There is, at present, no good argument for differential weighting of idiosyncrasies vs. convergences. So, I assume Evidential Weight.

<sup>30</sup> There is some debate over whether it is the ‘likelihood differences’, ‘likelihood ratios’ or some other measure that captures evidential weight (c.f. Eells and Fitelson 2002). For my point here, it does not matter which is correct insofar as the evidential weight of idiosyncrasies and convergences are equal.

### Likelihood Function (Binomial Distribution):

$$L(\theta|x) = \binom{n}{x} \theta^x (1 - \theta)^{n-x}$$

A binomial distribution has a single parameter,  $\theta$ , which, in our running example, specifies the probability of the next observation being an idiosyncrasy given the data (i.e.  $\Pr(\text{Idio}_{(n)}|\text{Data}) = \theta$ ). And, naturally, the probability of the next observation being a convergence would be  $\theta_C = 1 - \theta$ . In general, this likelihood function would generate a likelihood value for  $\theta$  given a body of evidence consisting of some number of idiosyncrasies versus some number of convergences. Plugging in the values from the example yields:

**Likelihood Function** ( $n = 100$ , 64 idiosyncrasies, 36 convergences):

$$L(\theta|64) = \binom{100}{64} \theta^{64} (1 - \theta)^{36}$$

This function outputs a likelihood for various  $\theta$ 's ranging from 0 to 1. In other words, it tells us the likelihood of hypotheses that specify, from 0 to 1, the probability of next observation being an idiosyncrasy given the body of data. For example, the hypothesis that states that probability of the next observation being an idiosyncrasy (given the data) is 0.5 has the likelihood of  $7.8861e-31$ . We can illustrate the function in the form of a graph (Fig. 2).

But how does the value of  $\theta$  relate to the degree of contingency? As mentioned, the value of  $\theta$  specifies the probability that the next observation will be an idiosyncrasy given the data. For example, if  $\theta = 0.50$ , then there is a 50% probability that the next observation is an idiosyncrasy within the modal range. This is tantamount to saying that evolutionary contingency is true to a degree of 0.5. When the ECT is said to vary in degrees, it is meant that there are different levels of repeatability (or robustness) within a domain. So, if contingency were to reign absolutely supreme in some domain, then the probability of the next observation being an idiosyncrasy is 1.0 (and a convergence is 0) in domain. In other words, contingency is so strong in that domain that the probability of getting any idiosyncrasies is certain (and convergences is 0). A hypothesis with the  $\theta$  of 1.0 thus corresponds to an ECT hypothesis that specifies contingency to the maximum. We can denote the absolute ECT (the hypothesis on the far right of the spectrum with a  $\theta$  of 1.0) as  $\text{ECT}_{(1.0)}$ . A milder ECT—say  $\text{ECT}_{(0.8)}$ —would have a  $\theta$  of 0.8 and the RVL would have a  $\theta$  of 0. In general, then, the probability that the next observation is an idiosyncrasy given some ECT hypothesis is: for any  $n$  and  $\theta$ ,  $\Pr(\text{IDIO}_{(n)}|\text{ECT}_{(\theta)}) = \theta$ .

Given the likelihood function in our running example, we now have the likelihoods of various hypotheses and their corresponding evidential support by the data. However, how do we determine which hypothesis has the highest likelihood given the data? In order to determine the maximum likelihood estimate, we need to find the derivative of the likelihood function with respect to  $\theta$  and set it equal to 0. Accordingly, the *maximum likelihood estimator* is  $\frac{x}{n}$  (see “Appendix” for workings). So, the hypothesis with the maximum likelihood in the example is  $\frac{64}{100} = 0.64$ , and  $\text{ECT}_{(0.64)}$  has the highest likelihood given the data (this result

is also quite intuitive). In other words, the hypothesis that makes the data most probable is an ECT that specifies contingency to degree of 0.64. Now, of course, a different hypothesis—say  $ECT_{(0.22)}$ —is also *compatible* with the data, but its likelihood would be significantly less than  $ECT_{(0.64)}$ . Comparatively speaking, given the Law of Likelihood, the body of evidence (i.e. 64 idiosyncrasies and 36 convergence) evidentially favours  $ECT_{(0.64)}$  over  $ECT_{(0.22)}$ . In fact, the data *most* evidentially supports  $ECT_{(0.64)}$ .

Lastly, the likelihood function has the virtue of increased accuracy as there is more data. The likelihood profile will be ‘wide’ for small sample sizes but become increasingly ‘narrower’ as there is more data. And, as there is more data, one can increasingly be more confident in probabilistically ruling out certain hypotheses on account of their comparative likelihoods. In the figure below, for example, as there is more data, the tail ends of the probability distribution become almost, probabilistically, impossible (Fig. 3).

As I see it, the likelihood function is quantitatively powerful, but it is only *just* a *modest* claim about comparative likelihoods. It provides a means of evaluating hypotheses on the contingency spectrum *given a single body of evidence* and under *certain conditions* (as with any statistical model). So, whilst the likelihood function may be correct, one may still reject the ECT by denying that there are, in fact, any true instances of idiosyncrasies. Such a strategy does not challenge the likelihood model itself but challenges the inputs (i.e. the data) of the model. In this way, the model is only as good as the evidence—false observations will hinder the effectiveness of the model.

Vermeij (2006), for example, severely doubts that there are true instances of unique evolution and attributes the purported singular evolution of 23 idiosyncrasies documented in the biological literature as due to ‘information loss over time’ (e.g. missing fossil data and the like). However, to be fair, Vermeij operates on an almost impossible standard of unique evolution. He requires that a trait’s evolution be singular in all time and all place. So, at best, Vermeij’s conclusion may be true of only an ECT that is indexed to all of time and space which is, plausibly, false. Contingency-theorists ought to count the number of idiosyncrasies, appropriately defined in their two dimensions, and convergences in a particular domain to determine the truth of contingency in that domain. If there turns out to be no idiosyncrasies at all, but lots of convergences, there one has the answer to the contingency question.

Secondly, it is important to be aware of what can be inferred from the likelihoods which is merely a tool for comparing hypotheses (i.e.  $ECT_{(\theta)}$ ) given a *single* body of evidence and does not represent  $\Pr(ECT_{(\theta)})$  or  $\Pr(ECT_{(\theta)} | IDIO \& CONV)$ . However, under a Bayesian framework, the likelihood ratio is equal to the Bayes factor (in favour of the ECT) and thus, is a component in the calculation of the conditional posterior probability. That is— one can take the product of the likelihood and the prior distribution to produce a posterior probability mass/density function for the ECT. Nonetheless, there would remain an issue of determining the prior probabilities—I leave this task and their century-long quibble to the Bayesians.

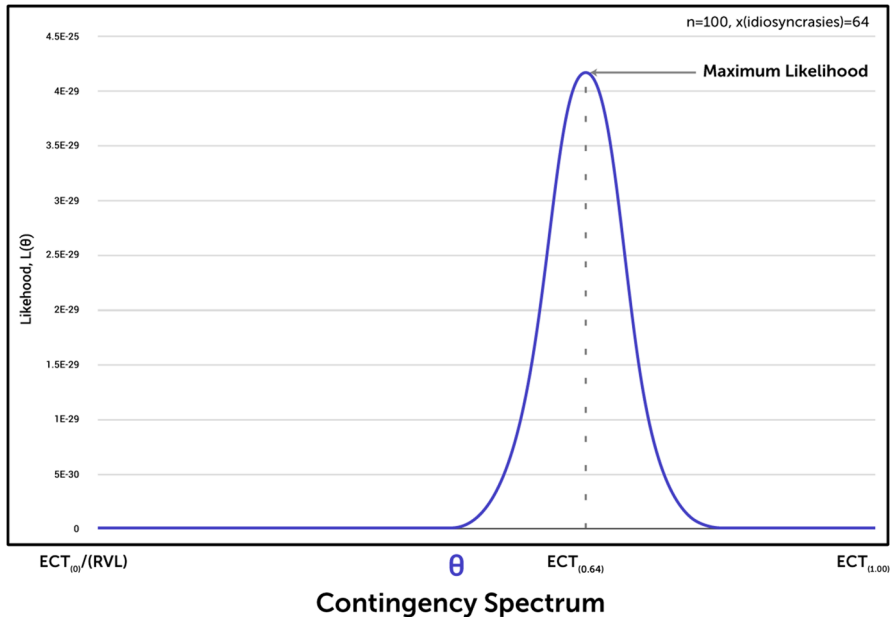


Fig. 2 Likelihood distribution for 64 idiosyncrasies and 36 convergences

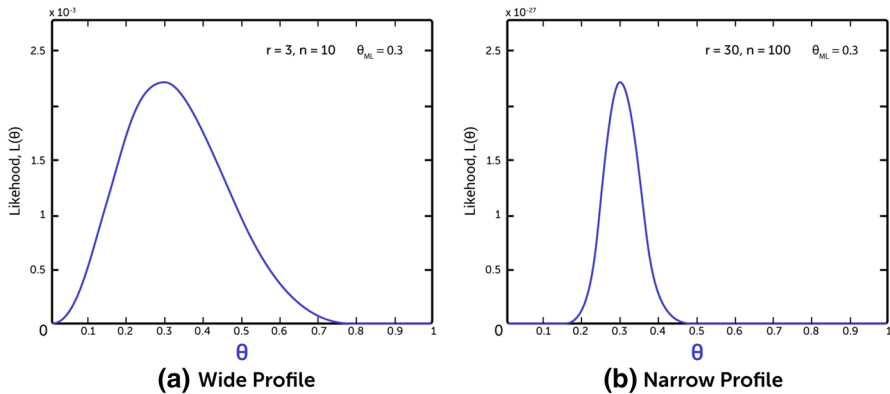
## Evolutionary idiosyncrasies as differential evidence

As established in “[Explanations for evolutionary idiosyncrasies](#)” section, idiosyncrasies undermine the robust view of life and support the ECT. However, evolutionary idiosyncrasies can differ in their degree of support for the ECT depending on certain statistical parameters revolving around their usage and a distinction between two different kinds of idiosyncrasies. Moreover, as mentioned at the outset, evolutionary idiosyncrasies can be defined and recognised according to two conceptual dimensions. An adjustment of either of these dimensions will shift idiosyncrasies’ evidential implications.

Firstly, the statistical power of arguments invoking idiosyncrasies can vary. This can be illustrated by *a numbers game*: suppose there is a series of evolutionary scenarios (varying or identical scenarios) where an idiosyncrasy arose. That is—within the series of evolutionary scenarios, there is a particular form that evolved only once. It would seem then that the greater number evolutionary scenarios—or alternative histories—in which the idiosyncrasy could evolve, the greater the support for the ECT. The thrust of this claim is found in the fact that given *so many* opportunities for a particular form’s evolution, it evolved *only once* (where as the number of opportunities increases, the argumentative power increases).

Take, for example, Lenski’s now infamous long term evolutionary experiment (LTEE). *E. coli* was known to metabolize only glucose as an energy source. However, when Lenski and his team grew twelve initially identical populations of *E. coli*, one of these populations soon evolved *aerobic citrate usage* (a peculiarity for *E. coli*





**Fig. 3** Wide versus narrow likelihood profiles

with some microbiologists even going as far as deeming it contrary to the very definition of *E. coli*; e.g. Koser 1924; Scheutz et al. 2005) at around the 30, 000 generation mark.

However, one can imagine a qualitatively similar experiment to that of Lenski's with the only difference being that instead of 12 identical populations, there were 12,000. If aerobic citrate usage still evolved only once despite a ten-thousand-fold increase in evolutionary opportunity, then this idiosyncrasy would have greater evidential strength for the ECT than an idiosyncrasy that arose from a lesser number of evolutionary opportunities (*ceteris paribus*). Thus, arguments from idiosyncrasies may do well to consider the number of alternative histories in which the idiosyncrasies could have evolved.

This is particularly important given that there appears to be, within the literature, certain contingency questions that are associated with a 'n=1' sampling issue. By a sampling issue, I mean that due to inappropriate sample size or structure, certain inferences about wider-regularities simply cannot be made. For example, one type of contingency question may ask whether the same biological forms are expected to evolve under different nomological systems (e.g. Beatty 1995). That is—if the laws governing evolutionary dynamics were different, would the same forms still evolve? However, given that we are privy to the only one nomology of our actual world, it is difficult to observe the existence of idiosyncrasies and convergences in alternative nomological systems<sup>31</sup> and hence, certain contingency questions may be a statistical non-starter in this respect. In other words, a radically wide modal range such as one across nomological systems may be prone to the so-called *coverage error*.<sup>32</sup>

<sup>31</sup> Some extrapolation about *similar* or *nomologically-consistent* systems may be possible but nonetheless difficult.

<sup>32</sup> The modal range may help in this respect by allowing the partitioning of a large series of evolutionary scenarios into individual lots of samples.

Secondly, a distinction can be made between two different kinds of idiosyncrasies: disparate idiosyncrasies (DPI) and divergent idiosyncrasies (DVI), whereby the latter has greater evidential strength for the ECT. In any modal range, divergent idiosyncrasies occur when two species share deep developmental homologues and yet arrive at distinct evolutionary outcomes of which at least one is uniquely evolved within the modal range. It demonstrates not only the unique evolution of an outcome but that evolutionary forces were sufficient to overcome phylogenetic and/or developmental constraints. In Lenski's experiment, for example, the populations were initially identical and, as such, had presumably identical developmental generators. It can then be inferred that any idiosyncratic outcome is then a divergence from similar starting points in developmental space. Divergent evolution is similar to parallel evolution in that there are shared developmental resources, but unlike parallel evolution in that divergences result in different outcomes rather than same outcome.

Disparate idiosyncrasies occur when two species *with different* developmental resources evolve distinct outcomes of which at least one is uniquely evolved. Disparate evolution is almost trivial in that it is not surprising that two different developmental starting points result in two different biological outcomes of which at least one is uniquely evolved within the modal range. It, however, serves as our contrast class to DVI.

This distinction between the two kinds of idiosyncrasies mirrors the CE versus PE distinction in that the division is based on whether there are shared developmental homologues (see Table 1). Interestingly, both distinctions attempt to tease apart two different sets of modalities: (i) the historical + nomological, and (ii) the merely nomological. That is—whereas genuine CE is the repetition of a form due solely to nomological considerations, PE is the result of both the historical and nomological.<sup>33</sup>

The distinction between divergent and disparate idiosyncrasies is meant to highlight the difference in the evidential role and strength that these idiosyncrasies play for the ECT. For instance, divergent idiosyncrasies answer adaptive hypotheses whilst disparate idiosyncrasies do not: instances of divergent idiosyncrasies show that phylogenetic constraints have been overcome since two species that were located closely in developmental space have now arrived at two different outcomes.

The distinction also shows that divergent and disparate idiosyncrasies are accounted for by different explanations. An explanation of divergent idiosyncrasy would appeal to natural selection being weak or contingent. On the other hand, divergent idiosyncrasies cannot appeal to *historicity* since its outcome descended from the similar starting points. Similarly, the strength of natural selection would be an irrelevant explanation for cases of disparate evolution: when two species with different developmental generators arrive at distinct outcomes, the strength of natural selection (whether weak or strong) cannot be inferred. This is owing to the fact that both weak and strong natural selection is consistent with the result that

<sup>33</sup> Recall that one of the major criticisms propelled against 'convergences' by the likes of Currie (2012b), Pearce (2012), Powell (2012), Powell and Mariscal (2015) was that instances of PE fail to constitute truly independent alternative histories of life due to shared developmental homologues, and thus, instances of PE are nonetheless privy to the same historical constraints whereas genuine CE escaped historical constraints to demonstrate true *independent* convergence. In the terms of my present analysis, PE fails to demonstrate repeated evolution *across* evolutionary systems in the modal range.

disparate evolution occurred. In these ways, divergent and disparate idiosyncrasies are accounted for by different explanations.

Thirdly, as previously mentioned, there are two conceptual dimensions in defining and recognising idiosyncrasies whereby an adjustment in any of these dimensions will result in a shift of idiosyncrasies' evidential target. In the remainder of this section, I will explain how a contingency-theorist can adjust these dimensions to suit their respective epistemic projects, so that any subsequently observed idiosyncrasy will be evidentially relevant to a particular contingency thesis of their concern.

Recall that the *scope of uniqueness* refers to the range of conditions (e.g. time, geographical space, or, nomology) in which an idiosyncrasy can obtain. As such, observations of idiosyncrasies defined with a considerably narrow scope of uniqueness will inform only the evolutionarily contingent dynamics of a correspondingly narrow modal range. This is to say that idiosyncrasies are informative only of an evolutionary contingency thesis with a modal range index that *corresponds* to the scope of uniqueness. Hence, if an epistemic agent adjusts the scope of uniqueness that they take idiosyncrasies to have, then any such recognised idiosyncrasies are supportive of an ECT with a different modal range index. So, if a contingency-theorist were specifically interested in the body morphologies of aquatic, swimming creatures within our galaxy (e.g. McGhee 2011), then they ought to look for uniquely evolved body morphologies within the right scope—namely, *across all planets within the galaxy*. Counting the number of idiosyncrasies with an ill-defined scope (say, of a different galaxy) will be evidentially mismatched.

Similarly, adjusting the subject of idiosyncrasy will also shift the evidential target of idiosyncrasies. One way to adjust the subject of idiosyncrasy is to invoke a different grain of analysis. But to elect a particular level of grain and to count the idiosyncrasies present at that level is informative of only evolutionary contingency that occurs at that level. For example, suppose a contingency-theorist counted certain extremely, fine-grained idiosyncrasies such as specific colour patterns of mimicry. That is—they looked at all cases of mimicry within a modal range and considered whether there were uniquely evolved colour patterns. Some colour patterns might genuinely be non-contingent since there may be robust reasons for their occurrence such as their need to resemble certain universal patterns in nature. Others colour patterns might genuinely be idiosyncratic—a *one-off* evolutionary event due to some of the aforementioned explanations. However, at this level of analysis, such fine-grained observations would inform only contingency questions about the repeatability at the level of colour patterns and says nothing about the coarser-grained regularity of Batesian or Mullerian mimicry. That is—the grain of idiosyncrasies must also correspond to the grain of the evolutionary contingency thesis in question.

Conversely, having an extremely coarse-grained resolution of idiosyncrasies will not only entail that few idiosyncrasies will be found, but that any such observations of idiosyncrasies will be supportive of only an equally coarse-grained ECT. Take predator avoidance, for example. This trait—on account of its coarse-grained characterisation—is likely to be multiply realisable. That is—specific physiology conducive for quick getaways from lurking predators, camouflage coats to conceal oneself, or, high intelligence may be considered 'predator avoidance' all the same. So, it is unlikely that genuine idiosyncrasies can be found at the level of 'predator avoidance'. However, if genuine idiosyncrasies can be found at this level, then it would be supportive of a specific

**Table 1** Types of independent and dependent evolution

	Independent evolution	Dependent evolution (Shared history)
Same outcome (‘Convergences’)	Convergent evolution	Parallel evolution
Different unique outcome (‘Idiosyncrasies’)	Disparate idiosyncrasy	Divergent idiosyncrasy

contingency thesis and one that is rather strong (and interesting)—i.e. the thesis that ‘predator avoidance’ is evolutionarily contingent trait. My contrasting of fine-grained versus coarse-grained resolutions is not to suggest that invoking certain levels of analysis are epistemically questionable endeavours, but merely that electing the grain of analysis is highly dependent on the epistemic agent’s interests since the grain of analysis is *evidentially specific*. So, when defining the grain of idiosyncrasy, consider the corresponding grain of the ECT that is of concern.

But instead of merely adjusting the grain of a trait, suppose that the subject of idiosyncrasy was, now, a particular *species*. This would be informative of only the evolutionary contingency of species and not traits. That is—it answers contingency questions about whether *species* are likely to be repeatedly found. Losos’s (2017) recognition of the platypus as an idiosyncrasy may be a good example of recognising *species* to be the subject of idiosyncrasy. This is because the striking features of the platypus, such as the mammalian egg laying, are not, themselves, uniquely evolved. After all, it is widely known that the echidna are mammalian creatures that also lay eggs. However, the platypus, as a whole, with its full complement of traits may plausibly be uniquely evolved. If Losos is right such that the platypus *qua species* is an idiosyncrasy, then the platypus may be an *evolutionarily contingent* form, after all, though its traits may not.

Like the scope of uniqueness, there must also be a match between the subject of idiosyncrasy and the subject of the ECT. Evolutionary contingency theses can differ in the subject that they take to be evolutionarily contingent. Theoretically, certain ECT’s refer to evolutionarily contingent traits whilst others can refer to evolutionarily contingent species, populations, etc. And so, in order for idiosyncrasies to be relevant to the contingency thesis in question, their subjects must correspond.

## Conclusion

Despite the title of this paper, there is not *the* one evolutionary contingency thesis, but an infinite number as differentiated by its modal range, subject (including grain), and, then, its degree of strength. Whichever variant of the ECT is of concern is dependent on the epistemic agent’s interests and the full specifications of the thesis, but the evidence—whether idiosyncratic or convergent—ought to also have the corresponding dimensions in order to be empirically tractable for the thesis at hand.

The concept of evolutionary idiosyncrasies, although previously overlooked, is crucial for making progress in the debate about evolutionary contingency. Not only

do idiosyncrasies serve as evidence in support of evolutionary contingency, but they can be invoked in further analyses to be pitted against convergences in order to pinpoint the relative significance and/or strength of contingency in a particular domain. Additionally, explanations for their occurrences are informative of the way in which evolutionary dynamics have failed to robustly produce biological forms. Thus, to preclude a consideration of this newfound concept would be a detriment to any contingency-theorist who wishes to determine the truth of evolutionary contingency.

By way of ending, I should say that none of these audacious praises is to imply that their occurrences are a given for that is very much an empirical matter. Rather, the point is that the presence of idiosyncrasies, *or lack thereof*, in a modal range can be telling of the truth of contingency. If a thoroughly exhaustive search results in nil idiosyncrasies observed, then evolution might, after all, be truly robust and replicable... for a particular modal range, anyways.

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## Appendix: Deriving the maximum likelihood estimator

Binomial likelihood function:

$$L(\theta|x) = \binom{n}{x} \theta^x (1 - \theta)^{n-x}$$

To find the maximum likelihood in a binomial distribution (when there are no saddles or minimum's), set the derivative of the likelihood function with respect to  $\theta$  to 0 (i.e. set the gradient to 0). However, it is quicker/easier to find  $dy/dx$  of the log of likelihood function which is:

$$\log L(\theta|x) = \log \binom{n}{x} + x \log \theta + (n - x) \log (1 - \theta)$$

Dy/dx of the log of likelihood function:

$$(\theta|x) = \frac{x}{\theta} + \frac{n-x}{1-\theta}(-1)$$

Now, set equal to 0 and re-arrange:

$$\frac{x}{\theta} = \frac{n-x}{1-\theta}$$

Therefore, maximum likelihood estimator:

$$\text{Max}\theta = \frac{x}{n}$$

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