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Discussions

Darwinian hydrology: can the methodology Charles Darwin pioneered help hydrologic science?

C. Harman[1] and P. A. Troch[2]

[1]Department of Geography and Environmental Engineering, Johns Hopkins University, Baltimore, Maryland, USA
[2]Department of Hydrology and Water Resources, University of Arizona, Tucson, Arizona, USA

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Correspondence to: C. Harman (charman1@jhu.edu)

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Abstract

There have been repeated calls for a Darwinian approach to hydrologic science or for a synthesis of Darwinian and Newtonian approaches, to deepen understanding the hydrologic system in the larger landscape context, and so develop a better basis for predictions now and in an uncertain future. But what exactly makes a Darwinian approach to hydrology "Darwinian"? While there have now been a number of discussions of Darwinian approaches, many referencing Harte (2002), the term is potentially a source of confusion while its connections to Darwin remain allusive rather than explicit.

Here we discuss the methods that Charles Darwin pioneered to understand a variety of complex systems in terms of their historical processes of change. We suggest that the Darwinian approach to hydrology follows his lead by focusing attention on the patterns of variation in populations, seeking hypotheses that explain these patterns in terms of the mechanisms and conditions that determine their historical development, using deduction and modeling to derive consequent hypotheses that follow from a proposed explanation, and critically testing these hypotheses against new observations. It is not sufficient to catalogue the patterns or predict them statistically. Nor is it sufficient for the explanations to amount to a "just-so" story not subject to critical analysis. Darwin's theories linked present-day variation to mechanisms that operated over history, and could be independently test and falsified by comparing new observations to the predictions of corollary hypotheses they generated.

With a Darwinian framework in mind it is easy to see that a great deal of hydrologic research has already been done that contributes to a Darwinian hydrology – whether deliberately or not. The various heuristic methods that Darwin used to develop explanatory theories – extrapolating mechanisms, space for time substitution, and looking for signatures of history – have direct application in hydrologic science. Some are already in use, while others are not and could be used to develop new insights.

Darwin sought explanatory theories that intelligibly connected disparate facts, that were testable and falsifiable, and that had fertile implications for further research. While

a synthesis of the Darwinian and Newtonian approaches remains a goal, the Darwinian approach to hydrologic science has significant value of its own The Darwinian hydrology that has been conducted already has not been coordinated or linked into a general body of theory and knowledge, but the time is ccoming when this will be possible.

> . . . In effect, what an immense addition to our knowledge of the laws of nature should we possess if a tithe of the facts dispersed in the Journals of observant travellers, in the Transactions of academies and learned societies, were collected together and judiciously arranged! From their very juxtaposition, plan, co-relation, and harmony, before unsuspected, would become instantly visible, or the causes of anomaly be rendered apparent; erroneous opinions would at once be detected; and new truths – satisfactory as such alone, or supplying corollaries of practical utility – be added to the mass of human knowledge. A better testimony to the justice of this remark can hardly be afforded than in the work before us – Mr. Darwin's "Structure and Distribution of Coral Reefs." (Jackson, 1842)

1 Introduction

The idea of a "synthesis of Darwinian and Newtonian worldviews" has been mentioned in a number of opinion papers (Sivapalan, 2003, 2005; Bloschl and Zehe, 2005; Beven, 2006; Kirchner, 2006; Newman et al., 2006; McDonnell et al., 2007; Wagener et al., 2010; King and Caylor, 2011; Kumar, 2011; Sivapalan et al., 2011b) and an increasing number of research papers (Sawicz et al., 2011; Cullis et al., 2012). The needs to predict and to understand watershed behavior in areas without long gauging records (Sivapalan, 2003) and under changing conditions (Sivapalan, 2012) requires new theories that go beyond the mechanics of runoff generation and focus on understanding the underlying climatic and landscape properties that control those mechanics (Sivapalan, 2005; McDonnell et al., 2007; Wagener et al., 2013; Thompson et al., 2013a). Wagener et al. (2013) argue for the need for a Darwinian approach for prediction in

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ungauged basins, and discuss many of the concepts and approaches that have been given the term "Darwinian". Many of these visions cite Harte (2002) as an inspiration, who suggested that Earth systems science needs new approaches to dealing with the formidable difficulties of global change. He suggested that new approaches ought to find a synthesis of the disciplinary world-views that dominate within physics (the "Newtonian" side) and ecology (the "Darwinian" counterpart). Elements of this synthesis would include simple, falsifiable models, the search for patterns and laws, and an embrace of "the science of place" – the in-depth examination of site-specific case studies.

So what is a "Darwinian" approach to hydrology? The threads of the "Newtonian" worldview whose aim is to develop "physically-based" models of hydrologic behavior with a level of precision approaching that of Newtonian mechanics or derived from Newtonian "first principles" itself can be clearly seen in a vast body of experimental, field, and modeling-based hydrologic science. (The textbook of Brutsaert, 2005, provides a thorough reference for the successful results of these efforts.) The brief discussion by Harte (2002) does not provide a sufficiently detailed description of the Darwinian worldview to make the idea of Darwinian hydrology unambiguous to those schooled in a Newtonian approach. Consequently there is a danger that the term "Darwinian hydrology" could be a source of confusion and misinterpretation. Darwin's work has itself been frequently misunderstood (often deliberately so) for more than 150 yr. It may appear that "Darwinian" is equivalent to "ecological" and that what is being called for is simply to pay greater attention to the role of biological processes in the hydrologic cycle, or perhaps to incorporate natural selection into hydrologic models somehow.

However, we argue that this is not the case. "Darwinian" hydrology represents a complementary set of questions about water and landscapes and an alternative set of approaches to answering those questions. Far from being a radical or new notion, many elements of the approach can be found in published studies, though the importance and connection of these studies to this larger purpose may not yet be clear or appreciated.

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This perspective on Darwinian hydrology is directly inspired by the work of Charles Darwin himself and can be illustrated by analogy to his body of work. To a number of evolutionary scientists, notably Ghiselin (1969) and Gould (1983) a key contribution of Darwin's work was his construction of a way of doing "historical" sciences that connected observations of current forms with mechanisms and processes operating over history (much of what follows is drawn from these references and from On the Origin of Species, Darwin, 1859, *The Formation of Vegetable Mould through the Action of Worms, with Observations on their Habits*, Darwin, 1881 and *The Structure and Distribution of Coral Reefs*, Darwin, 1842). As Gould (1983) notes, the results of historical change "lay strewn around us", but the processes that produced them are not so easily observed. Connecting structure and history through mechanisms, Gould (1983) posited, is "the quintessential problem of evolutionary theory: how do we use the anatomy, physiology, behavior, variation and geographic distribution of modern organisms, and the fossil remains in our geologic record, to infer the pathways of history". Replace the reference to organismal characteristics with those of watersheds and hydrologic systems, and this is the quintessential problem that we argue a Darwinian approach to hydrology could seek to answer: how do we use the observable structure and function in populations of watersheds to infer the pathways of their history. By doing so we might learn much about the unobserved structure and function today and as watersheds change into the future. "Evolution by natural selection" was the theory that Darwin proposed to explain the present day forms and their variation. But to focus solely on that (transcendent) theory is to miss the means by which Darwin arrived at it, and thus to miss the potential contribution of his way of thinking to hydrology: *methods* for understanding how the variety, distribution and contemporary function of hydrologic systems are determined by their historical evolution.

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2 The Darwinian method

While the idea of evolution is today popularly regarded as Darwin's great achievement, this opinion is erroneous in two important ways. First, the idea that evolution occurred at all was a "common heresy" at the time and had been proposed by Darwin's grandfather Erasmus amongst others (Gould, 1983). Secondly it overlooks the revolutionary approach to scientific inquiry that Darwin developed not only in *Origin* but throughout his whole career. It was Darwin's documentation of systematic geographic variations in species, his discovery and explanation of the mechanism by which evolution occurred, and the mountain of evidence that he amassed to support this mechanism, that are the key contributions of the *Origin of Species*.

It can be difficult today to comprehend the mindset that was dominant prior to Darwin, in large part because of the pervasiveness of the intellectual revolution he created. To those steeped in the modern scientific era, "natural selection" can seem so conceptually elegant and simple an idea that it is a wonder that it took so long to be discovered. Darwin's insight has naturally raised the question for historians and scientists alike: what was it about Darwin's scientific methodology that was so special and led to such breakthroughs? For our purposes we can ask: what of Darwin's methods are transferable to the study of watersheds that we might make breakthroughs of similar importance (at least within the modest confines of hydrologic science).

2.1 The type of question: anatomy vs. biogeography

The first thing to consider is the type of questions that Darwin chose to address. In many points in his career (not just in the study of evolution) Darwin was concerned with the documentation and explanation of the spatial variations in individuals of similar types. To give one non-ecological example from Darwin's earlier work in geology, he proposed an explanation for the spatial distribution of coral atolls, fringing reefs and barrier reefs (Darwin, 1842) for which alone he might have been justly renowned had his later work on species not overshadowed it. Threads of the same emphasis on the

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observation and explanation of variations in form connect across the many questions that Darwin addressed in his life.

Prior to Darwin, the question regarding species and their distribution was thought of very differently. Species were regarded as fixed types with an essential character that could be inferred by studying the anatomy of individuals of that type. This paradigm of *essentialism* was part of an intellectual tradition traceable to Plato's "ideal forms" – these ideas were widespread in every corner of intellectual inquiry at the time (Mayr, 1982). The scientific study of species tended to be largely concerned with documenting the essential characteristics of anatomy. For Darwin's contemporaries like Louis Agassiz, the characteristics were the design of the creator and variations around the ideal were mere imperfections. Furthermore, the distribution of species around the world (and the apparent appearance and disappearance of species in the geological record) was explained by localized special creation and extinction, in accordance with that design. The presence of mammals in Asia and marsupials in Australia was a brute fact: to be documented not to be explained. Biogeographic variations could be explained by post hoc rationalizations regarding the wisdom of the creator (who, wisely, gave polar bears white coats and forest-dwelling black bears dark coats).

Although initially Darwin accepted this paradigm, he came to be dissatisfied with it, since it provided no clear pathway for inquiry (Ghiselin, 1969). Instead he came to regard the variation of species in space and the variations of anatomy and habit within a species as both being of tremendous interest and importance. Darwin was a meticulous observer of the particulars of individual species' anatomy (indeed his mammoth treatise on the comparative anatomy of barnacles remains a benchmark of the field). However his theories on biogeography and evolution ultimately explained the variations within a species and between species. Darwin would not have developed such theories if his attention had been fixed on the observation of a single archetypal individual of a single species.

Compare these ideas to the study of watersheds. A large effort has been made to analyze the "anatomy" and "physiology" of watershed hydrologic systems, resulting in

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profound (but incomplete) insights into the spatio-temporal distribution of water storage and flux and the processes controlling runoff generation and water balance partitioning in individual watersheds. (It may be a stretch to regard such hydrologic processes as "Hortonian overland flow" and "saturation excess overland flow" as deriving from an essentialist impulse within hydrology – then again, it might not be. However, as Loague et al., 2010 point out, even though it is common to talk about these as distinct processes, it is not always possible to distinguish between them.) The dominant paradigm for understanding these processes is through the Newtonian physics (particularly the conservation equations) that are the foundation of our hydrologic models. These models attempt to capture the important processes that operate at the catchment scale (even though they implicitly assume that upscaling processes is possible through effective parameter values) and drive the focus of hydrologic science toward finding the correct parameter values through observations, field experiments and optimization algorithms. In this endeavor we are clueless about constraints on parameter combinations that may result from the co-evolution of the catchment properties, such as the ecosystems, soils, and topography.

So, we are left with no satisfying capacity to understand, let alone to predict, why a particular watershed developed the hydrologic system it did. The hydrologic functions of a watershed are largely understood as brute fact without historical origins. It should be emphasized that these origins do not only refer to the geomorphic evolution of the landscape over millions of years, since watershed hydrologic behavior is the result of geomorphic, pedogenic, ecologic and anthropogenic processes. While the disciplines that study these processes possess deep understanding of the origins of landscape form, ecosystems, soils, and so on, it is hard to point to an equivalent body of knowledge about the origins of the hydrologic system as a whole, as it integrates across all these histories. Observations and modeling of hydrologic fluxes in a watershed model can provide insights into their interactions, but are not explanations of their own origins, in the same sense that the observation of a kangaroo's pouch cannot on their own explain the origins of marsupials in Australia.

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What Darwin sought, and what a Darwinian hydrology can also seek, is an explanation of the origins of variations within populations. To do so however requires a type of "explanatory theory" that is quite different to the theory that is commonly used in hydrologic science.

2.2 Heuristics for developing explanatory theory

Many of the essential features of this type of explanatory theory can be introduced through examples of how Darwin developed specific theories throughout his life. Gould (1983) argued that, over the course of his career, Darwin employed three broad strategies for analyzing history in a scientific way: (1) measuring and extrapolating observable processes, (2) classification and space-for-time substitution, and (3) looking for the unique signatures of historical mechanisms embedded in present form. These are exemplified by his studies of earthworms (Darwin, 1881) of coral reefs (Darwin, 1842) and in the study of biogeography discussed at length in *Origin* (Darwin, 1859).

2.2.1 Measure and extrapolate the observable processes of change

A profound insight that Darwin's theories relied upon was that the slow accumulation of small causes could have world-shaping effects if given enough time. This insight came to him through the revolutionary geological works of Lyell (1830). In Darwin's final work on the formation of "vegetable mould" (what is today often called the O and A horizon of soils) Darwin made a careful study of the habits and distribution of earthworms (Darwin, 1881). He collected quantitative data on the mass of worm casts, the frequency with which individual worms transport soil to the surface and the density of worms themselves in the soil. He was thus able to establish a rate at which the whole mass of soil turned over (0.8 to 2.2 inches decade^{-1}). This analysis was not simply to document some peculiarities of worms but to present and test a hypothesis, namely that the rolling, fertile hills of the English countryside were in a state of constant churning by the action of earthworms. This churning explained a variety of other observations,

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including the smoothed form of the landscape, the tendency of stones placed in a field to sink over time and for stone fragments in the regolith to form up in lines parallel to the surface. Thus a range of observations was "explained" by the accumulation of the small – yet observable – actions by worms.

2.2.2 Classification and space-for-time substitution

Where the processes involved in the formation of a phenomena are not directly observable (either because they happen so slowly or intermittently or because they have ceased altogether) a different approach is needed. In one of his first great achievements as a geologist, Darwin proposed a theory about the structure of coral reefs surrounding tropical islands (Darwin, 1842). He began with a classification of their forms that distinguished fringing reefs that occur on the shore, barrier reefs that are separated from the shore by a lagoon, and coral atolls, in which a ring of coral surrounds a lagoon without an island. These, he argued represent a progression of forms that would occur if an island were thrust up from the sea-floor and subsequently subsided or eroded away. The coral ring that begins as a fringing reef is preserved in the subsequent forms so long as the rate of sea-floor subsidence is slower than the maximum rate at which the coral can grow upwards. This space-for-time substitution argument is based on the assumption that similar phenomena (like reef formation) recur and follow similar "evolutionary trajectories" with different starting times. If disparate phenomena can be classified and arranged in this way from young to old, we can see through history.

Today radiometric dating techniques exist that can reveal whether different places do indeed represent a progression in time. However Darwin's theory was widely popular even before such techniques were available because his theory is rich in corollary implications that provide critical tests of its validity. The outer sides of coral atolls should plunge steeply to the sea floor. Atolls should be rare or absent in areas of uplift. In areas of rapid subsidence we should find remnant towers of coral that grew too slowly and were drowned. The theory was accepted not simply because this time-for-space substitution provided a coherent story uniting one set of observations, but because it

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made specific predictions that have been subsequently confirmed by other observations.

2.2.3 Look for unique signatures of historical conditions

Darwin accumulated evidence for or against an explanatory theory even if processes could not be measured directly or if the uniqueness of each individual defied classification. Even before developing the theory of natural selection to explain how species change over time, he had developed a sophisticated theory explaining biogeographic variations in species distribution based on their dispersal mechanisms and the way geological change created (or removed) barriers to dispersal. During his voyage on the Beagle, Darwin observed that amphibians (whose eggs can only survive in freshwater) are entirely absent from Pacific islands, and that the only mammals present are flying bats. Darwin experimented on seeds to see which could survive long periods submersed in seawater or passing through the guts of birds. He was able to show that the assemblage of species in a place depended on the particular history of barriers to species reaching that place (such as oceans or mountain ranges) and the particular mechanisms available to those species for crossing those barriers (by flight, migration over land, or rafting across the ocean).

Darwin's theory of biogeography was developed by finding a coherent explanation for a wide variety of facts about a particular place that relied – as much as possible – on only those facts that could be observed or determined experimentally. It is an approach that acknowledges the unique history that has controlled the development of each place (whether geology or colonization), without giving up on the ability to construct an explanation whose features are transferable between places. In this case, transferability comes from the ability of the theory to suggest *where to look* when constructing an explanation of a unique place: towards the formation of migratory barriers and the propagation and dispersal capacities of species.

These three approaches are "heuristics" in the sense that they suggest a way of tackling a problem. They do not define the Darwinian approach, and there are other methods that could be included. But all share the characteristic that they seek to explain observed variations in form and function in terms of historical mechanisms and in ways that are transferrable between places. Furthermore, these approaches suggest methods for testing them against further observation.

2.3 Testing explanatory theory with the hypothetico-deductive method

So how can such theories be tested, given that we are unable to "rewind the clock" and watch the evolution of organisms, coral reefs or watersheds directly? These problems are ubiquitous in those Earth sciences that aim to explain origins (including geomorphology and pedology), and the examples above show that they were of great interest to Darwin. Although there has been debate about the type of scientific reasoning Darwin employed (and his own statements are sometimes contradictory) Ghiselin (1969) argued convincingly that Darwin's almost compulsive theorizing and hypothesizing is a key component of his success, despite his occasional public claims about being a "pure Baconian" inductionist (Ayala, 2009). The hypothetico-deductive approach that Ghiselin (1969) argues Darwin used can be approximated as four steps: (1) collect a vast amount of detailed observations of the pattern to be explained, (2) conceive a hypothesis that accounts for as many of the observations as possible, (3) derive from this hypothesis a consequent set of circumstances that must also hold if the hypothesis is true (this is the step that gives the method its name), and (4) critically test whether these consequences do hold. This approach blends the epistemological approaches of induction (step 1), abduction (step 2), deduction (step 3) and falsifiability (step 4). Kleinhans et al. (2010) has already argued for the combination of these approaches for developing "explanatory models" in experimental hydrologic science that explain the general phenomena under consideration rather than make specific predictions as accurately as possible.

It is difficult to give a precise definition of the epistemological characteristics of an "explanatory theory" (and probably unnecessary for our purposes so long as its objective can be stated with sufficient clarity). However such theories make predictions

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about more than one place (otherwise they are of little general interest), but these predictions are in character conditional and statistical: they posit that under certain conditions (corals growing around an island being actively uplifted), some outcomes (fringing reefs) are more likely than others (coral atolls). The predictions made by such a theory are probabilistic in a mode similar to statistical mechanics but operate on far smaller populations subject to a more complex set of conditions than an ideal gas, and are thus much more prone to unforeseeable deviations from the central tendency.

Vitally important to Darwin and to the proposed Darwinian approach to hydrology is the requirement that explanatory theories not be merely good stories that, post hoc, provide a plausible explanation for the observations. To Darwin, the invocation of artifices for which there is no evidence was a fatal flaw in the theories of his contemporaries. This principle extended beyond his rejection of special creation where its application is obvious. Many of Darwin's contemporaries invoked the appearance and disappearance of land-bridges to explain anomalies in the biogeographic distribution of species. Darwin saw these as theoretical luxuries for lazy scientists, and he insisted on devising and testing his theories on the basis of the present configuration of continents (Wegener's theory of plate-tectonics was still decades away). Recently physicist David Deutsch has made a similar argument that a central quality of a good explanatory theory (in addition to being falsifiable) is that its conditions are "hard to vary" without the whole argument collapsing – conditions cannot simply be added or removed (like hypothetical land-bridges) in the face of contradictory facts (Deutsch, 2009).

Thus a proposed explanatory theory supersedes an existing one if it can explain more facts with fewer conditions. The most compelling evidence for natural selection in *Origin* (Darwin, 1859) came largely from its ability to explain variations between species (including biogeographic variation) better than any competing theory and do so in a way that was rich in implication (Ghiselin, 1969). Note that Darwin's theory was not built around a theory of genetics, as he was unaware of Mendel's theory of inheritance – the arguments for evolution were not built on "first principles" but rather on empirical observation. Exceptions and anomalies are inevitable; no theory will be

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able to explain all the observations perfectly, and such exceptions should not be merely accommodated by the invocation of causes without evidence. Exceptions to a rule demand their own explanation and drive the search for better theory.

These characteristics – the ability to connect intelligibly across disparate facts, to be testable and falsifiable, and to lead to new horizons for further research – make the explanatory theory of Darwinian thought so useful and valuable despite its limited ability to make precise predictions in the same way as a Newtonian prediction.

3 A Darwinian approach to watershed science

Translated into hydrologic science, Darwin's methods suggest an approach to watershed science that differs from the Newtonian approach in the kinds of questions it asks about landscapes and in the tools used to answer those questions. The Darwinian approach aims to provide an explanation – derived from the historical co-evolution of the landscape and the legacies of the past over many timescales (from geological to human) – for the patterns of variation in hydrologic behavior within a population of watersheds. Following the hypothetico-deductive approach to science that Darwin advocated, this explanation cannot be a "just so" story, but rather elucidates a mechanism and generates testable corollary hypotheses about the landscape including, but not exclusive to, its hydrologic behavior. To be judged superior to competing hypotheses, this explanation must account for more variation with fewer happenstance contingencies and exceptions.

With this framework in mind, it is not hard to find examples of recent hydrologic studies that contribute towards such a theory, even where that goal is not articulated. In the discussion below some of these will be highlighted, though a comprehensive review must be left for another time.

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3.1 Hydrologic variations in populations of watersheds: regimes filters and functional patterns

What are the patterns of hydrologic variability that a Darwinian approach aims to explain? Darwin was able to measure and compare the properties of organisms (such as the length of a finch's beak), but it is not so simple to define the hydrologic "form" of a watershed, let alone compare these forms in a consistent way between watersheds. Comparing the hydrology of two watersheds distant from each other on the basis of (for instance) only their streamflow today is of very little interest – the Newtonian physically-based models are better suited to "explaining" why one may have greater flow than the other in terms of the antecedent conditions and recent rainfall. The response of a watershed to a single storm event does little to reveal the hydrologic "anatomy and physiology" of a watershed. A Darwinian approach to hydrology might better try to explain hydrologic variability viewed with a broader perspective in terms of hydrologic regimes, filters, and functional patterns.

3.1.1 Variation across time: regimes and filtering

The (broadly speaking) statistical distribution of hydrologic states and fluxes over a larger time and space scale has been referred to as a system's *regime* (Pickup and Warner, 1976; Mosley, 1981; Magilligan and Nislow, 2005). This structure has been investigated through the prism of signatures including the flood frequency curve (e.g., Robinson and Sivapalan, 1997), water balance partitioning (Troch et al., 2009; Harman et al., 2011; Sivapalan et al., 2011a), flow duration curve (Coopersmith et al., 2012; Yaeger et al., 2012; e.g., Ye and Sivapalan, 2012; Ye et al., 2012), recession curve (e.g., Wittenberg, 2003), preferred states in the soil moisture distribution (e.g., Western and Grayson, 2001) and seasonal variations in the fluxes measured at an eddy-flux tower (Thompson et al., 2013b). The study of regimes adopts the Darwinian approach of analyzing populations but in the temporal domain (understanding a population of events within a watershed).

It might be argued that hydrologic regimes are largely determined by climate, leaving little variation left over to be "explained". Indeed the studies cited above show that climate is the major control on most of the signatures of catchment regime. However, this control is expressed in two different ways: directly, through the water and energy drivers of the water balance, and indirectly as one of many controls on the evolution of the landscape's hydrologic properties. Methods have been (and continue to be) developed to extract the net effect of these properties at the watershed scale from the observed hydrologic signatures (e.g., Wittenberg, 1999; Jothityangkoon and Sivapalan, 2009; Kirchner, 2009), many derived from the notion of a "top-down" approach to conceptualizing hydrologic systems (Klemeš, 1983; Sivapalan et al., 2003). By separating the direct effects of climatic variability from the "filter" that transforms that variability into the hydrologic regime, these methods can reveal watershed hydrologic properties explicable in terms of their history, including the indirect effects of climate (e.g., Troch et al., 2013). The analysis of the passive tracer and biogeochemical "filtering" extends this type of integrated-scale analysis (e.g., Guan et al., 2011).

While data on hydrologic fluxes are essential to quantifying these regimes, reliable observations of fluxes at watershed scales are limited to streamflow, though estimates of precipitation in particular are improving. Because of this limited window, watershed models have been relied on to "fill-in" the unobserved data and provide a richer view of the hydrologic regimes. For instance, Carrillo et al. (2011) used a model calibrated to hydrologic signatures in 12 watersheds to extract a set of timescales that controlled different sets of storage and partitioning processes, such as the duration of infiltration at the average storm rainfall rate that would be required to fill the unsaturated zone and initiate deeper drainage. Expressing catchment characteristics in terms of timescales helped reveal how the variations in those characteristics between watersheds determine variations in watershed regimes.

However, these models inevitably incorporate a-priori assumptions about the nature of the controls and the way to express these controls in a mathematical model. The regimes of internal fluxes and states are therefore dependent on the assumed model

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structure and on the parameters obtained by calibration. As Beven (2000) and many others have discussed, the problems of equifinality and parameter identification limits our ability to use models to resolve the unique character of individual watersheds. Poor model structures can rarely be discriminated on the basis of the available hydrologic data, let alone identification of the "best" structure and parameter set to represent the watershed. It has been suggested that rather than producing a sharp image of the unique hydrologic regime of a specific watershed, inversion from hydrologic data can only reveal an ill-defined cloud of regimes that corresponds to the subset of models that have been judged "behavioral" within the space of possible models (Beven, 2000). Limitations on our ability to directly observe hydrologic storage and flux at both high spatial and temporal resolution and large spatial extent therefore mean that we are left with a "blurry", uncertain image of watershed anatomy and behavior, heavily laden with the theories that we aim to improve upon.

3.1.2 Variation across places: functional patterns

The true potential of the Darwinian approach is to explain and even predict the patterns of variation in regimes and filtering between places. The importance of "comparative hydrology" for advancing hydrologic understanding and theory has been discussed for many years (Falkenmark and Chapman, 1989). Patterns in the regimes and filtering of many watersheds across climatic, geologic and ecologic gradients have been called "functional patterns" (Sivapalan, 2012) since they suggest emergent functional interdependencies between hydrologic behavior and the landscape properties that control them

We can highlight two fundamental and illustrative example of the kind of functional pattern in the regimes of watersheds that might be explained by the Darwinian approach, (1) variations in average annual water balance partitioning and (2) variations in runoff process dominance.

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3.2 Water balance

The Budyko curve, popularized by Budyko (1974) plots the fraction of average annual precipitation (P) that leaves the watershed as evapotranspiration (E) against the ratio of energy available to drive evapotranspiration (Ep) and available water (P). When data from many watersheds are plotted together on this curve, variations in this hydrologic partitioning of annual precipitation into runoff and evapotranspiration in natural watersheds are limited to a curve near the upper envelope of possible values constrained by the available water and energy. There is no (Newtonian) constraint that prevents the population of watersheds from completely and randomly filling the space within the envelope defined by these conservation constraints. The fact that they follow some sort of curve, even with considerable scatter, suggests that the associations between the controls on water-balance are not random but are a signature of the climate and development of the landscape.

This curve has been examined by a number of modeling and observational studies (Milly, 1994; Zhang et al., 2001; Atkinson, 2002; Farmer et al., 2003; Porporato et al., 2004; Donohue et al., 2007; Yokoo et al., 2008; Gentine et al., 2012; Troch et al., 2013) that have elucidated the first-order controls on this partitioning. These suggest that for a given ratio of Ep/P the variation between watersheds (that is, the scatter around the curve) is largely controlled by a number of factors that can be summarized as

- the temporal variability of inputs of precipitation and energy, including the phasing of the seasonal variability in rainfall and energy, the frequency and intensity of storm events, and their tendency to cluster in time.

- the capacity of the landscape to store these inputs (in canopy interception, soil, perched water tables, and deeper groundwater) and delay their delivery to the watershed outlet.

- the ability of vegetation to access this stored water during periods of high atmospheric demand through root water uptake.

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At the extreme upper envelope bounding the Budyko curve are watersheds where seasonality in energy and water inputs directly covary, storage capacity is high, and vegetation is always able to access the needed water. At the lower boundary (along the horizontal axis) are watersheds where rainfall occurs at times when there is little energy to drive evapotranspiration, storage capacity is low and water runs off quickly, and that water which is stored is unavailable to vegetation.

Understanding these controls on the water balance partitioning is not trivial and continues to be an active area of research. The elucidation of hydrologic controls on water-balance partitioning is a step towards an explanatory theory of why those controls vary between landscapes and towards the further goal of predicting variation between places. Such a theory would provide answers to fundamental questions, like why does a particular watershed have the storage capacity that it does? How has the geologic, pedogenic and geomorphic – and indeed hydrologic – history of that landscape determined that capacity? Recent attention to the role of storage in watersheds (McNamara et al., 2011; Tetzlaff et al., 2011) has typically avoided the question of how and why that storage exists.

3.3 Process dominance

Runoff generation mechanisms are generally conceptualized as Hortonian infiltration excess "Dunne"-type saturation excess, and subsurface stormflow. The tendency of a watershed to be dominated by one mechanism over another is a function of the physical properties of the landscape and the climate, and understanding these controls is central to getting the "right answers for the right reasons" (Kirchner, 2006). Measurement and modeling can be used to determine which processes control runoff generation in a particular watershed, but there is little in the way of theory to make quantitative prediction about variations in process dominance between watersheds.

Dunne (1978) attempted to synthesize, in a qualitative way, the controls on runoff generation process dominance at the hillslope scale. The "Dunne Diagram" as it has come to be known proposed that in dry or human-impacted watersheds, the Hortonian

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mechanism dominated, while in more humid and densely vegetated areas, runoff generated depended more strongly on topography and soils. In steep areas with permeable soils, subsurface stormflow was the dominant mechanism, while in low-gradient areas with concave foot-slopes, saturation excess held sway.

Despite the influential nature of this conceptualization of the patterns of variation in runoff generation between watersheds, there have been few attempts to either arrive at a more precise, quantified form of it or to develop a theory that explained why these systematic variations in process dominance occur. As with the Budyko curve, there is no reason why naturally-developed watersheds should cluster into these patterns – a human-created asphalt car-park in a wet climate can violate both the Budyko curve and the Dunne diagram without violating conservation of mass, energy and momentum. That non-human-created watersheds show such a pattern of behavior is a pattern that must be explained using tools that go beyond fluid mechanics or soil physics

3.4 Darwinian explanatory hypotheses for watersheds

A Darwinian explanatory theory is necessarily circumspect, yet provides a clear picture of why variations in the regimes or filtering observed in a region exist. Recent work by Lohse and Dietrich (2005) (see also Lohse, 2002) and Jefferson et al. (2010) suggests that such a coherent explanatory hypothesis can be developed to account for changes in hydrologic function along an "evolutionary pathway" of basaltic rocks in Hawaii and in the Oregon Cascades. Each study made detailed observations of soils and hydrologic flowpaths in a variety of soils formed on lava flows ranging in age from the Holocene to more than one million years old. In both sites the evidence suggested that the young landscapes were initially drained vertically through the bedrock and into groundwater and so groundwater discharge was significant. At older sites the soils became increasingly weathered to produce illuviated clay horizons, which tended to reduce vertical infiltration and promote lateral redistribution. Jefferson (2010) noted a systematic decrease in the baseflow index as watersheds aged. This shift in hydrologic process dominance was accompanied by an increase in the drainage density and morphology of hillslopes (similar patterns were perceptible in Hawaii also, K. Lohse, personal communication, 2012).

These studies point toward a hypothesis about the ways that hydrologic processes evolve over time under wet climates with specific geologic initial conditions (basalt lava flows). A more general hypotheses could be framed to account for the functional patterns observed across many such landscapes, such that the frequency with which a given set of watershed characteristics is observed reflects (A) the frequency that the initial conditions leading along an evolutionary pathway to that combination is created (in the above case, the historical frequency of lava flows over time), and (B) to the relative rates of change of landscapes in different configurations (which appears to slow down over time in the case of Jefferson, 2010).

The first part of this more general hypothesis reflects the requirement that the present hydrologic configuration of the landscape must be "reachable" in the state-space of possible hydrologic configurations that evolve as a result of the available geomorphic, ecologic, pedogenic and anthropogenic processes. The second suggests that the relative frequency with which a particular combination of watershed characteristics is observed (given some constraints of climate and geology) is influenced by the relative duration that such a combination of parameters can persist in the face of geomorphic, ecologic, climatic and even human processes of change.

This is an elementary hypothesis, derived from the assumption that some combinations of hydrologic properties are inherently unstable and prone to rapid shifts (geologically speaking) towards more stable states. Other combinations are more stable, in the sense that they persist for a longer period of time. This assumption is supported by ideas regarding the persistence of and convergence towards geomorphic "forms" (Brunsden and Thornes, 1979) and the resilience and stability of ecosystems (Tucker and Hancock, 2010), both of which posit that there are system configurations that persist while others are transient. The stable configurations of landscapes need not be static nor even steady-state under this assumption – they need only to have

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combinations of process dominance and water-balance partitioning that change more slowly over time than other combinations.

Thermodynamic "optimality" constraints have been suggested as a basis for predicting watershed behavior (Kleidon and Schymanski, 2008; Schymanski, 2008; Schymanski et al., 2009), under the hypothesis that watershed organization represents a configuration that optimizes a thermodynamically defined condition. The hypothesis presented here makes fewer assumptions than the optimality hypotheses but is potentially compatible with them. That is, it is possible that the combinations of watershed properties that engender the most rapid change may be those that are furthest from the optimal conditions. Conversely, the most persistent states may reflect an asymptotic approach to the optimal condition or possibly an optimal condition perturbed by disturbance, rather than the optimal itself (such as where frequent fire in grasslands prevent recruitment of trees, even though from a water-use perspective they might be closer to an optimal condition). However, optimality is not a necessary outcome of change over time, nor a necessary characteristic of persistent states.

This hypothesis is also appealing in part because of its resemblance to statistical mechanics, which can predict the aggregate properties of a population of molecules in a gas (like temperature) in terms of the most likely combination of particle states. Along these lines, we could express the hypothesis equivalently as proposing a sort of "ergodicity" in landscape: that the frequencies with which a set of combinations are observed in a region (that is, when watersheds with similar climatic and geologic properties are compared) are related to the frequency with which they occur and to the duration that they persist in time (that is, when the evolutionary history of a single watershed is considered). Combinations that can persist only for a short period of time (or are the transient consequence of an infrequent disturbance) are less common today than those that persist for a long time (or arise from a frequent type of disturbance).

As it is stated here, this is a very general hypothesis and needs considerable development to meet the standards of a Darwinian explanatory theory. However it does have the necessary characteristics of such a theory, as described above. It connects

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across disparate facts by proposing a connection between geomorphic and ecologic landscape stability and the frequency of different regimes of hydrologic variability and process dominance. It is testable, in that the relationship between relative stability and relative frequency can be compared, at least in principle. This comparison will be challenging in practice. Finally, it motivates new approaches to develop and test this type of Darwinian theory.

3.5 The Darwinian method in watershed hydrology

So how could the methods that Darwin used to develop and test his explanatory theories be applied to watershed hydrology to test explanatory theories like the (very general) one presented above? The three methods described earlier are not the only ones possible in the "Darwinian Hydrology" framework, but they serve as potentially fruitful avenues for research, and so are worth exploring in more detail.

3.5.1 Extrapolating mechanisms: coevolution modeling

As Darwin did in his studies of worms, it is possible to extrapolate from detailed measurements of rates of processes (like worm castings transported to the surface) to the structures that arise from the accumulated effects of those processes. Advances in geomorphic modeling in recent years (Roering et al., 1999; Dietrich et al., 2003; Pelletier and Rasmussen, 2009) have created the capacity to connect the local processes of sediment redistribution and the larger-scale landscape structure. As these theories have matured, they have naturally enough become increasingly linked to models of soil and ecosystem development and to the climatic drivers (Paola et al., 2006; Hancock et al., 2011; Pelletier et al., 2013). For example, Heimsath (1997, 2005) connects soil and landform development to provide mechanisms that simultaneously "explain" the variations in hillslope curvature and soil thickness between landscapes (Roering, 2008). Many of these theories are based on a philosophy articulated in Dietrich et al. (2003) that aims to develop process representations that have

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measurableparameters, make specific predictions (such as the form of a slope-area relationship) that can be tested against observation, and are applicable at the scale of the problem – that is, the time and space scales relevant to the formation of landscape morphology.

Models that aim to predict the co-evolution of the hydrologic "morphology" of landscapes – the regimes and the functional patterns between places – might have a similar set of aims. Rather than being used to predict the future evolution of landscapes or reproduce the precise form of a particular landscape, these models allow hypotheses to be tested about the relationship between the cumulative effects of processes interacting over time and in space. As Thompson et al. (2013b) suggest, this co-evolution modeling is not limited to landform and soil evolution over geologic timescales but can include the development of ecological and human coupled systems, if the appropriate parameterizations can be developed and properly tested. Such models could help evaluate the "reachability" requirement of the Darwinian hypothesis and quantify the relative duration of different configurations of landscapes. There are great challenges to be overcome in finding the appropriate ways to represent the feedbacks between hydrology and other longer-term landscape processes and in the parameterization of these relationships from observations, but progress is being made (Hopp et al., 2009; Tucker and Hancock, 2010). For example, Pelletier et al. (2013) recently circumvented these feedbacks by connecting effective process parameters to a higher-order variable (Effective Energy and Mass Transfer – EEMT) that captures water and energy constraints on landscape-forming processes and used this to explain variations in topography soil thickness, land forms and biomass across a climate gradient in Southern Arizona.

3.5.2 Space-for-time: a genetic classification of watersheds

Darwin's theories generally did not make predictions about the fates of individuals, but instead focused on the behavior of populations of similar types – be they species, coral reefs, or soils. The theories themselves were necessarily inter-dependent on the method of classifying those types in a useful way. Hydrologists have also been working to develop a classification system that can provide useful information about catchment function (McDonnell and Woods, 2004; Wagener et al., 2007). Many of these classifications are derived from the hydrologic behavior itself, either through analysis of characteristic signatures of rainfall and flow variability (Sawicz et al., 2011) or through bottom-up analysis of watershed hydrologic function using simple models (Carrillo et al., 2011). Others classify watersheds within a region on the basis of ecological, climatic, geologic, and land-use characteristics under the assumption that these will be the primary controls on hydrologic function (Winter, 2001; Woods, 2004).

These approaches highlight functional patterns and distinguish between watersheds that behave in fundamentally different ways (snow-dominated versus monsoonal, for example). They may provide breakthroughs to advance predictability in ungauged basins. However they do not yet perform the same function that Darwin's classifications did. Classifications based on observable characteristics can be described (to borrow a term from biological taxonomy) as phenotypical – they discriminate on the basis of present-day expressed morphology.

In contrast, Darwin's explanatory theories of coral reefs and organisms were built on a classification system that collected together functionally similar entities in a way that also grouped them in terms of their evolutionary origins. In modern terms, this connects the classification on the basis of present-day observable features (phenotypes) to classification on the basis of linked historical developments that have created those features (genotypes). This type of genotypical classification is tightly linked to the explanatory theory. In principle, since there are many ways to classify the different types of (say) coral reefs that exist, there is no reason to divide them into atolls, fringing reefs and barrier reefs (as opposed to some other grouping). However doing so immediately reveals a pattern in space connected to rates of sea floor uplift and subsidence. The ability of the explanatory theory to provide a unity of phenotypical and genotypical classifications contributes to the theory's success.

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A hydrologic classification of a similar type could be linked in the same way to an understanding of the type of evolutionary progression that produced it. Watersheds that have similar histories, and have converged through co-evolution into a similar set of characteristic behaviors would be grouped closer together (such as those that bear a strong signature of recent glaciation or those formed by the continuous adjustment of hillslope colluvial processes to changes in base level). Similarly, two watersheds whose hydrologic behaviors are superficially similar but arise from a very different set of histories (in the sense of "convergent evolution") would be grouped separately (as dolphins and fish are). This type of classification would enrich the picture of process dominance developed by Dunne (1978) by providing a hypothesis about the connection between the spatial patterns of process dominance and the progression of hydrologic forms a landscape passes through as it evolves.

3.5.3 Signatures of history: looking for evidence of general laws in detailed case studies

Just as Darwin's theory of biogeography did not make specific predictions about what the species of a place would be but rather about "what to look for" when investigating a specific place, so can a hydrologic Darwinian theory help determine what types of historical events might be of significance in shaping the contemporary hydrology of a watershed. For instance, Bain et al. (2012) have described the importance of appreciating historical legacies when interpreting landscape properties and estimating material flux rates in study sites. They caution that in many parts of the eastern US, estimates of "background" sediment flux rates from long-term studies may be biased by the legacy of structural changes in the landscape that followed European settlement but preceded the initiation of long-term monitoring.

Where neither rates of processes could be reliably quantified nor classification and space-for-time substitution used to provide insight, Darwin's detailed case studies provided a weight of evidence to support his general hypotheses. Within hydrology there are now a large number of watersheds that have been studied and characterized "in

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depth". Attempts at synthesizing these into a single framework have had only partial success. A corollary of the Darwinian hypothesis suggested here, testable by such case studies is that the configurations that produce water-balance relations far from the Budyko curve or combinations of process dominance in contradiction with the Dunne Diagram are either unstable configurations or configurations that are slow to change but rarely occur. For example, landscapes in humid climates whose soils induce rapid overland flow are hypothesized to undergo rapid geomorphic change. Such landscapes do exist, such as the Pink Cliffs near Heathcote in Victoria, Australia, where human disturbance (in the form of hydraulic sluicing during the Gold Rush period) perturbed the previous soil landscape configuration and exposed the weathered granite bedrock beneath. This area is now a rapidly eroding badland and will quickly (geologically speaking) disappear from the landscape. Similarly, vegetation quickly transforms areas where water is a limiting factor and is underutilized, even if disturbance or other factors prevent systems from obtaining an "optimum" configuration.

4 Conclusions

4.1 The promise of a Darwinian approach

We have argued that the methodological approach of Charles Darwin can provide lessons for the development of a "Darwinian" approach to hydrology. This approach is by no means a "panacea" to all the challenges hydrology faces (it will do little to improve observations of storage fluctuations at watershed scales, for instance) but could lead to new fundamental and practical insights.

The crucial step that Darwin made was to study not merely the physiology of individual species but the variations in physiology through space and time. The methods he developed to critically test hypotheses that explain these variations in terms of their natural history have arguably been as important to the history of science as his theory of natural selection. We argue that the study of populations of watersheds, and the search

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for an “explanatory theory” that connects their current similarities and differences to the processes that created them, is an essential aim of a “Darwinian” approach to hydrology. As Kleinhans et al. (2010) put it recently “In geology and biology an explanation for a phenomenon is not complete without reference to both physical factors and history”. This statement is in contrast with much of hydrology, in which watershed behaviors are documented ahistorically, as brute facts.

The Darwinian approach should not be confused with superficially persuasive ad hoc explanations about the holistic interactions that appear to control the regimes of watershed behavior. The explanatory theories put forward to account for the functional patterns in hydrologic regimes and filtering must be critically tested by observation. They should also unite a wide variety of previously disconnected facts, should be testable and falsifiable against observed data, and should provide abundant avenues for future research. Nor is the ability of regionalization techniques to predict the parameters of a hydrologic model or hydrologic properties (like the flood frequency distribution) equivalent to explaining those variations in a “Darwinian” way. Darwin sought theories that not only predicted the patterns in the present spatial distribution of things but also connected that distribution to the historical processes that created them. It should also be obvious that a Darwinian “explanatory theory” is not simply a landscape evolution model (e.g., Willgoose et al., 1991; Dietrich et al., 2003; Pelletier et al., 2013) (though these have a role, as discussed above), nor is landform evolution the only type of hydrologic development amenable to the Darwinian mode. For instance the work by Di Baldassarre et al. (2009) on the connection between contemporary flooding and historical floodplain development and management (see also Castellarin et al., 2010; Di Baldassarre et al., 2010) can be seen as following the “Darwinian” mold of seeking historical explanations for present-day variations. Srinivasan et al. (2012)’s classification of syndromes of water crises is based on common mechanisms of causation and could be regarded as “genetic” within the Darwinian framework.

Darwinian theories could find practical application where they can constrain the combination of watershed properties and hydrologic behavior likely to occur in an area.

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There is currently no basis in well-tested theory for deciding whether a parameterized watershed model could plausibly have come into existence or for deciding the probability that it does exist based on landscape evolution This concept might be given a more formal definition. Consider the historical watershed evolution as a trajectory in "landscape space" with each point along this trajectory mapping to a behavioral subset of the "model space" of the system at a point in time (Beven, 2002). In control systems theory subspaces of the state space of a dynamical system are defined as "reachable" if there exists a control input that can move the system into them from an initial condition. In the language of Bayesian approaches to model uncertainty, the prior distributions of watershed model parameters are not currently constrained by the reachability of the model subspaces they represent. Such additional constraints might be of some use in modeling applications.

4.2 You may already be a Darwinian!

Elements of the Darwinian approach to hydrology can be found in the studies cited above and in many other works not cited. These works variously contribute to the characterization of the hydrologic anatomy and physiology in the sense of hydrologic regimes, filtering, and functional patterns, understanding of the mechanisms that shape the hydrologic properties of landscapes through time, classification and analysis of the patterns of variation in watersheds in space, and a large number of highly characterized experimental watersheds, each of which has been studied largely independently of the others. These efforts have not been coordinated though, and the links between them have yet to be made in many cases. Great insights may come when the connections between these individual studies are investigated in a coordinated way.

The search for explanatory theory in the "Darwinian" approach includes or extends many of the suggestions of McDonnell et al. (2007). It echoes the call to understand "why" the heterogeneity and structure of watersheds exist, and to link this understanding to observable "functional traits" and watershed function. In contrast though, the Darwinian approach suggests that this understanding can be obtained by investigating

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the processes of historical development and change that give rise to the heterogeneity, rather than focusing solely on the contemporary properties and behavior. We also advocate for an approach to classification that aims to unify genotypic and phenotypic approaches. The search for scaling and emergent behavior, including network and optimality principles is compatible with a Darwinian approach that seeks to explain the origin of these patterns in the processes that create them. These theories are complementary: a proposed optimality theory for hydrology will gain in credibility and usefulness if the historical progression that gives rise to it can be explained and used to define the set of watersheds where it will likely apply.

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