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Charles H. Smith

Western Kentucky University, charles.smith@wku.edu

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Alfred Russel Wallace, past and future

Charles H. Smith

Western Kentucky University, Library Public Services, Bowling Green, USA

ABSTRACT

The naturalist Alfred Russel Wallace (1823–1913) has for many years been standing in the shadow of his more famed co-discoverer of the principle of natural selection, Charles Darwin. Despite outward similarities between the two men's formulation of the principle, Wallace had fit his appreciation of natural selection into views on evolution that were quite different from Darwin's. A closer examination of what Wallace had in mind suggests a model of process in which natural selection *per se* acts as the negative feedback mechanism (actually, a 'state-space') in the relation between population and environment, and environmental engagement as made possible by the resulting selection of traits acts as the positive feedback part of the cycle. Thus, it may be better to contextualize adaptive structures as entropy-relaying biogeochemical facilitators that only 'generate a potential for evolution' than to portray them as the end results of evolution. This systems point of view better lends itself to appreciations of the biogeographical context of evolution than does the tree-thinking of a more conventional style of speciation-focused Darwinism, which sometimes confuses process with result.

*Correspondence: Charles H. Smith, Western Kentucky University, Library Public Services, Bowling Green, KY 42101, USA
E-mail: charles.smith@wku.edu

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That an international biogeography society should name an award after Alfred Russel Wallace (1823–1913) is both natural and appropriate: he is, after all, the acknowledged 'father' of the modern study of the subject (or at the very least of zoogeography, one of its two main subdivisions). That being so, there are probably very few among us here who are not at least generally familiar with his life and contributions in this realm. Very briefly, it was Wallace who, along with Darwin, gave us the model – natural selection – that sustains a dynamic view of the subject; he also made fundamental contributions to a variety of more specific studies, for example: the nature of island biotas, the process of corridor dispersal, the connection between glacial epochs and distribution patterns, the relation of river barriers to species divergence, the systematic study of

regional biotas, and – last but not least – astrobiology, and in particular the ecoclimatological study of extraterrestrial surface environments. We should perhaps additionally remind ourselves that many observers also regard Wallace not only as the leading tropical regions naturalist in history, but perhaps, in more general terms yet, as its pre-eminent field biologist overall.

Instead of dwelling on the obvious, I would prefer to focus here on what I personally feel is Wallace's most important legacy for biogeographical studies: one which, I submit, does not reduce to a matter of history alone. This concerns how he was able to bring together historical and ecological approaches to the study of biogeography – and in a fashion capable of sustaining a logical process of investigation not only into the twentieth century, but on to the twenty-first as well. To understand how Wallace came to such a synthesis, we need return ourselves to his days as a young naturalist, traipsing through the tropical forests of the Amazon and Malay Archipelago.

At that point – the early and mid-1850s – Wallace was pursuing a research program that hinged on one understanding that most observers of today, knowing what we know of

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his later writings, should find surprising. Specifically, he was operating under the assumption that characteristic organismal traits were *not* necessarily functionally utilitarian. Two or three of his early writings are quite clear on this score (see especially Wallace, 1853, 1856); he probably felt this way largely because it appeared that to embrace notions of necessary function was to support a view of a preordained existence akin to, or exactly the same as, a first causes-based creationism. What, then, was his provisional working model of how the evolution of species proceeded? Although the evidence is not yet absolutely conclusive, he appears to have adopted a *final* causes-based scheme – one that looked to some fairly subtle or remote environmental influence as pulling the strings. In this understanding, individual adaptations were to a certain degree incidental, coming into being for unknown reasons, and then promoted or overturned by forces extending well beyond the level of populations, much less individual organisms.

An environmentally deterministic presence of this type might be expected to relay various signs of its enactment through the characteristic results of distribution and adaptation it yielded, so Wallace made it his business to look for such. When in good time he felt he had accumulated enough evidence to characterize one such result – the spatial-temporal pattern of divergence of species lines – he issued the paper ‘On the Law Which Has Regulated the Introduction of New Species’ (Wallace, 1855). This featured his famous ‘Sarawak law’, the notion that ‘Every species has come into existence coincident both in space and time with a pre-existing closely allied species’. The essence of this law, which many have marked as the dawn of modern biogeographical studies, has sometimes been forgotten: far from being a prescription for dispersalism, it is more the archetypal example of tree-thinking. Some might argue, therefore (and some have: see, for example, Michaux, 1991), that it looks ahead more to the dawn of vicariance biogeography studies than it does to the kind of thinking expressed by later workers such as Matthew and Simpson.

A reminder, however, that despite his embrace of this principle – which we still endorse today – Wallace was not yet at this point a believer in the necessary utility of adaptive characters. In a little-known paper on the orangutan published a year *after* the Sarawak essay, he continues to state in the most explicit terms his belief that many adaptive structures have no functional value:

Do you mean to assert, then, some of my readers will indignantly ask, that this animal, or any animal, is provided with organs which are of no use to it? Yes, we reply, we do mean to assert that many animals are provided with organs and appendages which serve no material or physical purpose. The extraordinary excrescences of many insects, the fantastic and many-coloured plumes which adorn certain birds, the excessively developed horns in some of the antelopes, the colours and infinitely modified forms of many flower-petals, are all cases, for an explanation of which we must look to

some general principle far more recondite than a simple relation to the necessities of the individual (Wallace, 1856, p. 30).

Obviously, something was going to have to give. Wallace had for all intensive purposes shown through his Sarawak law that evolution did in fact take place, but so far all he had was an inductive demonstration of its results, and no model of ecological or population dynamics that could *explain* those results. Wallace had always recognized the importance of morphological features in characterizing the basic differences among species, of course, but apparently he was still expecting to identify a final cause that bore ultimate responsibility for guiding the longer-term fates of these various outcomes. Much later, in his autobiography *My life* (Wallace, 1905, Vol. 1, p. 360), he would refer to this time as a period during which he believed it would be impossible to understand how and why every individual adaptation had come about: seemingly, no one causal process could be held responsible.

Then, in early 1858, during a bout with malaria, and while he was thinking about the writings of Thomas Malthus on population controls, the solution came to him. It was simple, actually: as he had thought, adaptations were not preordained; there was enough variation within every population to respond adaptively to the multi-causal constraints and opportunities afforded by environment, and enough time to allow all the relative probabilities of operationalization success to play themselves out.

Now a man named Charles Darwin had experienced a not wholly dissimilar revelation some years earlier, and as events transpired it was Darwin who would end up monopolizing the stage in the theatre of nineteenth and twentieth century evolutionary studies. And while it is true that the two men’s conceptualizations of the principle had much in common, there are also important differences between the Darwinian and Wallacean versions of natural selection – including one which, I now suggest, will ultimately go in Wallace’s favour.

Darwin, though no mean observer of living things, tended to think linearly – more like a geologist than an ecologist or geographer – when pondering the mysteries of organic change. Indeed, ‘tree-thinking’ was his forte, and he could not help but look upon the key concept of adaptation as both a process and a result. To this day we are dominated by this view that evolution as a process yields particulate results – individual adaptations, creatures and species populations – that stick out like so many little twigs on the great metaphorical tree of life. Darwin and his followers have been criticized for this alleged circularity in their reasoning – even the phylogenetic systematists, the ‘twiggiest’ of all evolutionists, are guarded on the matter, sometimes disowning (or maybe ignoring) the more contentious specifics of Darwinian theory and preferring to dwell, Wallace-like, on objective facts of specimen morphology and location in space and time. So far no one has seen any pressing need to abandon the greater good to respond to this apparent lesser evil.

By contrast, in Wallace’s model of natural selection – even after 1858 – there actually is no implied *process* of adaptation:

there is only the logical *result* of being adapted. For Wallace, adaptation represents a state-space: the logical implication of the interplay of variation, over-achieving reproduction rates and finitely limited resources. Actually, he usually referred to his brainchild as the 'law' of natural selection, a usage we do not see much these days. [Note in this context his attempt to 'demonstrate' (his word) the origin of species by natural selection through the logic of necessary result on p. 302 of his book *Contributions to the theory of natural selection* (Wallace, 1870)]. Wallace also has endured a lot of criticism for his approach, most notably in the form of accusations of hyperselectionism raised by historical science-focused naturalists like the late Stephen Jay Gould. But this ambush is not really fair, as Wallace only reasoned that the whole of the evolutionary process passed through the natural selection filter, and not that natural selection itself *initiated* it. In fact, he pointed out on many occasions that we were largely ignorant of the laws that govern the origin of variation, and it reasonably can be argued that all those subsequent theories and discoveries that have been viewed as possibly overturning natural selection – e.g., mutation theory, Mendelism and more lately molecular evolution – are no more than realizations of our efforts to expose inherent causes of the type he alluded to.

For many years 'Darwin versus Wallace' debates over various particulars of evolutionary theory focused on other matters, many of which are of limited direct interest to biogeographers: sexual selection, for example, and whether natural selection can explain the existence of humankind's higher faculties. Then, in 1972, some hint of a possible new order arose from a rather unlikely source: an anthropologist exploring some elements of the then still-emerging science of cybernetics. Gregory Bateson, remembering some intriguing passages in Wallace's Ternate essay likening the action of natural selection to a governor on a steam engine (Wallace, 1858, p. 62), remarked in his *Steps to an ecology of the mind* (Bateson, 1972, p. 435):

The steam engine with a governor is simply a circular train of causal events, with somewhere a link in that chain such that the more of something, the less of the next thing in the circuit...If causal chains with that general characteristic are provided with energy, the result will be...a self-corrective system. Wallace, in fact, proposed the first cybernetic model...Basically these systems are always *conservative*...in such systems changes occur to conserve the truth of some descriptive statement, some component of the *status quo*. Wallace saw the matter correctly, and natural selection acts primarily to keep the species unvarying...

Bateson was not content to let the matter go at that. Later, in the collection *Mind and nature: a necessary unity*, he added the following observations (Bateson, 1979, p. 43):

If it had been Wallace instead of Darwin [who started the trend], we would have had a very different theory of evolution today. The whole cybernetic movement might

have occurred one hundred years earlier as a result of Wallace's comparison between the steam engine with a governor and the process of natural selection...

Bateson makes a very interesting point here, but he neglects an important issue: clearly, models of the general evolutionary program cannot rest *entirely* on negative feedback-based mechanisms and explanations; it is ultimately the breaking away from such recursive constraints that by definition leads to novel development. Had Bateson dug a bit further he would have discovered that the evolutionary relationship between negative and positive feedback relations had already been explored some years earlier in an important work titled 'The second cybernetics: deviation-amplifying mutual causal processes' (Maruyama, 1963). In this milestone paper Magoroh Maruyama describes how the information imported to an organism from the environment mediates two kinds of feedback: deviation-counteracting processes (negative feedbacks) which tend to enforce equilibrium conditions, and deviation-amplifying processes (positive feedbacks), which cause systems to change in directions either of greater or of lesser order. While Maruyama's perspective helps us understand how a living system might be looked at as being either or both equilibrium conserving and equilibrium counteracting, it still does not specify the conditions under which directions of 'greater or lesser order' might be obtained; that is, what is it in the longer term evolutionary sense that tips the scales in favour of greater order?

This question leads us back to Wallace, and an opportunity to re-examine some fundamental aspects of the relation between biogeography and natural selection. We can begin by entertaining the notion that Wallace's initial struggle to understand the adaptive process might have been due to his early inability to distinguish between the negative and positive feedback components of the system. As Bateson pointed out, the 'governor-like' action of selective forces on existing adaptations has the effect, over generations, of weeding out poorly adapted individuals – an effect whose cumulating results may be seen in changes in morphology at the individual level. Historically speaking, one might describe this as 'evolutionary change' or the 'evolution of adaptations', but unless one can show at the level of the process itself why such change need be negentropy-accumulating, we are left only with an ecological reality: that adaptive structures are but the focus of the *negative* feedback part of the cycle, operationalizing an organismal state-space through which energy sources at the surface of the earth are temporarily diverted and captured, applied to do chemical and physical work, and then returned in degraded form to the physical environment envelope (and ultimately out into space), maximizing system entropy. From this perspective adaptations are little more than one – though admittedly complex – interface in the biogeochemical cycling process.

Accepting this, one is inclined to wonder whether Wallace's early preoccupation with identifying large scale, environment-level forcing functions that could drive evolution might still

make sense. Adaptive *structures* aside, it would appear to be the realization of adaptive *potential* – the entry into new ecological involvements through organismal/population behaviour, movement, and dispersal – that represents the positive feedback part of the cycle leading to evolution. Because they are not one-dimensional entities, organisms/populations can and do enter into new associations with their environment, the result being the sorting out of gene pools into new adaptive structures. Some of these are adaptive in the short term sense but not in the longer term sense, producing overspecialization and, ultimately, dead-ends: extinction (an example of a deviation-amplifying trend resulting in a reduction of order). Others turn out to be adaptive across both time scales, supporting a flexibility of genetics and structure that leads to serial phylogenesis (a deviation-amplifying process yielding longer-term, larger-scale, diversification, and thus higher levels of order).

Recall that Wallace seems to have had in mind an evolutionary process subservient to final causes. In his own words, the ‘changes of organic forms’ are ‘to keep them in harmony with the changed conditions’ (i.e. of the environment, characterized very generally) (Wallace, 1870, p. 302). We are not accustomed to thinking in such terms in biogeography, but it may be time to reconsider our position. It should be apparent from the variety of stances taken by proponents of the anthropic and Gaia hypotheses that, philosophically speaking, the ‘final causes’ concept has produced the gamut of teleological mind-sets. We need not, however, adopt the more extreme of these to imagine how a system as described here could find its way to higher levels of order. Suppose, for example, that the environment as it physically extends away from any given individual organism inherently presents statistically greater survival probabilities in some directions than in others. On this basis, individuals – and more importantly, populations – might tend to disperse in some spatial directions more easily than in others.

Further suppose that these survival probabilities are set by the level of optimality of delivery, directly, and indirectly, of certain very basic resources – for example, and most probably, water – to the adaptive structures of the organisms mediating energy transfer through the system. If this is so, perhaps the degree of specification of selection required to fit into the less ideal environments in this respect will be more than that required to fit into more ideal ones: that is, that because there is too much or too little of something vital at certain times and places, a good deal more selection must go into establishing adaptations that will continue to support morphostasis in those places. This latter kind of selection will tend to produce the kinds of specialized organisms whose populations will be at greater risk should the environment change markedly at some future point.

‘Optimality’ of delivery of resources must involve one further consideration, however: how efficiently the living structure supported can be turned over within the local ecosystem for continuing re-use. The cycle of life and death in any community is such as to influence the turnover rate of vital

resources in the local ecosystem. Temperature governs the rate of biological modification at the molecular level, but here too there is an optimum, as too great a deviation from the mean is bound to have negative effects on the nature of stability at the community level. If one couples a surplus of water with a considerably higher than average mean ambient temperature, for example, a little noted kind of stress on community organization is imposed. Under these conditions in tropical rain forests, great surpluses of water combined with high temperatures produce leaching rates that keep soils depleted of nutrients. The effect of this stress has been to force a community structure in which most of the vital nutrients in the system are kept locked up in inaccessible biomass at any given time: they cannot be leached out of the system, but neither can they be turned over quickly enough to support productivity levels that match, for example, those of mid-latitude grassland systems.

The preceding sketch describes what can be interpreted as a mild form of final causation. In theory, as a population grows, it should first find it easier to spread out in directions of lower environmental stress as here portrayed, since the conservative ‘governing function’ of selection (à la Wallace) to fit in will not be as severe as in areas of high stress. Thus, the suggestion is that *all* populations will tend to disperse in the same preferred directions, in so doing non-randomly perpetuating genetic flexibility – and, importantly, contributing to the shaping of ever-more stable and resilient biogeochemical pathways. This is evolution – environmentally mediated (or even directed) evolution, to be sure, but not environmentally *determined* evolution: again, as in Wallace’s thinking, that which is selected for to meet the challenge in any given instance constitutes *whatever* can be genetically sorted out, in large part by trial and error, to support persistence.

In the mid-1980s I applied this line of reasoning in my PhD thesis (Smith, 1984) and a follow-up paper (Smith, 1986) in some detail. Not much came of the effort at the time; however, as this was a period dominated by discussions on other ideas – notably, non-equilibrium evolution, vicariance biogeography and molecular evolution. In the two works just mentioned, I suggested three immediate reasons why an emphasis on this ‘evolution as spatial interaction’ notion might be a preferable starting point for complex environmental studies to ‘adaptation-as-evolution’ approaches. These considerations still, I think, are worthy of reflection:

1. To begin with, we are provided with means lending themselves equally well to either state-space or process modelling efforts. As part of a discussion concerning the non-equilibrium theory of biological evolution proposed by E. O. Wiley and Dan Brooks in the 1980s (Wiley & Brooks, 1982; Brooks & Wiley, 1986), Wicken (1983, p. 442) remarked that:

...internal ordering depends on a system’s ability to export entropy to its environment...The virtue of the thermodynamic approach to evolution is its ability to connect life *ecologically* to the rest of nature through

shared matter and energy flows; denying the ecological component of evolution, or the influence of ecology on development, badly weakens (their) thermodynamic base.

Wiley and Brooks's theory, though provoking a good deal of discussion over the years, has seemingly run its course. They continued to defend it vigorously for a time; regarding the matter of the effect of ecology on evolution they only claimed to be 'rejecting ecological determinism' (Brooks & Wiley, 1985, p. 94). In the understanding expressed here, the environment does provide a forcing function, but this is viewed as implemented at the community, rather than individual, level. The environment can, I submit, effect direct control over what kinds of spatial interaction processes operate *among* organisms but only very indirectly, in the terminology of Brooks & Wiley (1985, p. 93), over the way each population's 'phase space defining the maximum number of microstates which the evolving lineage could occupy' changes with time (since this phase space is, as Brooks and Wiley themselves would argue, locked in as a function of the particular constraints and potentials developed over the line's own history, as 'summarized' at any given time within its gene pool). Outside variables (i.e., environmental delivery of vital resources) may thus be interpreted as defining the state-space within which organisms find themselves in the immediate sense, but not in such a fashion as to subvert the 'individuality' of development of any given evolutionary line. This overall causal structure has the obvious advantage of lending itself to ecological state-space description in which the controlling variables may also be understood to produce change in a way that need not be viewed as the kind of 'ecological determinism' that Brooks and Wiley object to.

2. This portrayal of the complementary – but still entirely separable – roles of spatial interaction and adaptation solves outright the philosophical dilemma attending the earlier mentioned complaint that in Darwinian thinking evolution involves a process (adaptation) yielding structures (adaptation) of non-independent definition (Ghiselin, 1966; Grene, 1971; Gould & Lewontin, 1979; Brookfield, 1982). As Lewontin (1984, pp. 237–238) has put it, 'The process is *adaptation* and the end result is the state of being *adapted* ... The problem is how species can be at all times both adapting and adapted'. When evolution is understood as the characteristics of change in the spatial interaction regime at the community/environment level (and not 'the process of adaptation'), the role of adaptive *structures* can be viewed as strictly ecological, providing a straightforward causal picture devoid of circularity and attending logical difficulties. In this role, adaptations are regarded simply (as described earlier) as structural attributes matched to environmental throughput: they mediate energy degradation, or, as Wicken (1983, p. 440) has put it, 'provide a means by which potential energy can be converted to thermal entropy and released to space'.

3. Further, re-interpreting evolution as a spatial interaction process provides a response to the complaint that the study of

the 'evolution' of adaptations (i.e. phylogenetic studies) reduces to idiographic 'narrative' (Gould, 1961). Particular adaptations are still regarded, of course, as arising in response to one-of-a-kind combinations of environmental and biological circumstances; given ever-increasing complexity of genetic constraints on the way change can be implemented, we should expect the exact manner in which potential energy is converted to thermal entropy to remain individually unique to each population. Again, this understanding – focusing on the homeostatic function of adaptation – resists any systematic biological interpretation beyond the identification of when and where each novelty arose (and the *post hoc* narrative sequencing of this information with all other such information). But when the homeorhetic function of adaptive structures – spatial interaction – is emphasized, such criticism is rendered moot. Following this interpretation makes it possible to think of irreversible processes as leading to more than the unique structures we call adaptations. Specifically, it in addition allows us to consider standing interaction patterns interpretable on normative grounds: in the biological sense, as competition/natural selection, and in the spatial sense, as statistically interpretable multi-species distribution patterns [in effect, an answer to Eldredge's (1981) complaints regarding the 'just so' nature of much of descriptive biogeography]. Like individual organisms, species populations (and their particular constituent adaptive arrays) eventually die and disappear – entirely – as functional (ecological) entities; not necessarily so, communities and ecosystems, that are more likely either to modify in place, or be forced to disperse *en masse*.

To these three points two more may be added – briefly. First, as it may be admitted that with respect to adaptive structures evolution historically proceeds randomly (or at the least, stochastically), it is likely the case that predictive modelling based on this focus will always be limited to identifying the *immediate* causal conditions involved. Wallace's original dilemma as to the means of origination of adaptations is thus likely to be a permanent one. We can, of course, identify certain classes of immediate results (such as mimetic resemblance), or use any number of kinds of experimental frameworks to relate specific cause to specific outcome – and in turn manipulate particular processes to serve our immediate ends (as, for example, in various medical contexts) – but there remains the real problem that trying to generalize this manipulation to the level of natural process is extremely tedious, as no state-space common to all relevant factors can ever be isolated. By contrast, if one regards the environment as an information field across which populations disperse, and with which they become integrated, one can begin to look at process in terms of relative rates and directions of change *in space*. If in fact such information fields exist in nature – related most elementally, as I have suggested, to certain optimalities in the rates of provision of fundamental resources – then one should be able to identify population-level traits that have developed in response to them. In my Dissertation (Smith, 1984) I made a first pass attempt at this. Variations in

soil moisture levels over the central United States of America constituted the 'resource' variable studied; this was combined with a similarly varying turnover-related multiplier based on ambient temperatures (via Van't Hoff's law) to produce a geographically varying indicator of eco-/evolutionary stress. Reasoning that populations should disperse preferentially according to the shape of this 'stress field', I examined range boundary records for the over five hundred species of mammals and herptiles occurring in the study area for evidence of such an effect, and in fact found some fairly good confirming evidence. Since that time much better distributional data and means of manipulating them have become available, and more elaborate tests could be performed. Further, and more importantly, tests of this kind could also be applied to particular spatial patterns of gene flow within individual populations (i.e., clinal analyses).

As a second point, and as suggested by comments made earlier regarding differences in selection regimes, the kind of approach advocated here could be instrumental in clarifying our understanding of the relation between *r*- and *K*-kinds of selection. Obviously, if evolution really is directly related to how certain fundamental resources are made regularly available for procurement and retained and recycled, this influence will find its way into all manner of associations between adaptive strategy and the organism's surroundings. In some instances, for example, life's economy may be dictated by seasonalities; in others, an ease in finding hosts. Trophic level organization, morphology and life histories should also show signs of such influence.

In recent years many investigators have been attempting to model spatial variation in diversity patterns by looking to the possible associative influence of a range of independent environmental variables: climate, soil moisture, ecological complexity, energy levels and so forth (see, for example, Kerr & Packer, 1997; O'Brien, 1998; Hawkins *et al.*, 2003; Hawkins & Porter, 2003). So far these efforts have lacked the dynamic modelling perspective that allows them to do more than correlate certain diversity characteristics with particular ambient environmental conditions. These are not, therefore, evolutionary models as they now stand, but it would not take much re-orientation to turn them into such. Efforts of this kind might give us a much more interactive view of the meaning of biodiversity, and at the same time allow us to follow Wallace's original lead and understand that there really is no generalizable 'process of adaptation'. We need to pay less attention to the 'twigs' themselves, and more to how they generate actions eventually playing out in space and time as responses to final causes inherent in the environmental delivery system.

A full one hundred and fifty years have now passed since Wallace's 'Sarawak law' essay of early 1855 put us at the brink of a biogeographical understanding that might have formed the very central element of a symmetrically logical evolutionary theory. Only three years later Wallace came up with the key remaining piece of the puzzle, but to no avail: Darwin's conception of adaptation-as-evolution – tree-thinking – was

quickly to assume dominance on the stage of evolutionary theorizing, and continues to do so today. There are signs, however, that things may be changing. One immediate result of the biodiversity studies movement has been the realization that a biology (or conservation program) dominated by independent investigations of individual species does not bring us a level of understanding of the biosphere that will ultimately be informative enough to preserve it. It appears that we are, whether we care to acknowledge it or not, increasingly on a search for final causes in the theatre of life. Alfred Russel Wallace embraced this ideal so many years ago, and though he had few theoretical vehicles through which he could express this orientation, every fibre of his intellect was committed to it. We cannot do better than to honour and affirm his commitment through the connection of his name with our own goals, both through commemorations of the type we are taking part in this day, and through continuing efforts to explore and extend his ideas.

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BIOSKETCH

Charles H. Smith is Professor of Library Public Services at Western Kentucky University, Bowling Green. His research interests include subjects in the history of science, evolutionary theory, biogeography, bibliography and general systems theory. He is the author or editor of *Alfred Russel Wallace* (1991), *Biodiversity studies: a bibliographic review* (2000), and *Alfred Russel Wallace: writings on evolution 1843–1912* (2004), and maintains the web sites ‘The Alfred Russel Wallace Page’, ‘Early Classics in Biogeography’ and ‘Some Biogeographers, Evolutionists and Ecologists: Chrono-Biographical Sketches’.

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