

Ontology of areas of endemism

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ABSTRACT

Areas of endemism have been recognized as important units in historical biogeography, and much attention has been given to methods of identifying these units operationally. Interestingly, little has been written about the philosophical nature of areas of endemism. The purpose of this essay is to make an ontological argument for areas of endemism as individuals and to discuss the consequences of such a conclusion. The recognition of species as individuals is crucial to the argument. Several criteria are identified for entities to be considered individuals, all of which are shown for areas of endemism. An ontological concept of an area of endemism is presented. Two of the consequences of regarding areas of endemism as individuals are that areas of endemism should be the preferred units of biogeography over the units used in event-based methods and that parsimony analysis of endemism and similar methods may be operational tools for the discovery of areas of endemism.

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INTRODUCTION

One of the key observations about the distribution of life on Earth is that it is non-random in space and time. Description of these spatio-temporal patterns represents the data of biogeography, and explanation of these spatio-temporal patterns has driven the development of the science of biogeography. Perhaps the concept most associated with the description of distributions is *endemism*, which can be defined as being endemic, or being restricted, to a particular distribution (see Anderson, 1994 for an excellent review of the history of the term). Based on previous work, *areas of endemism* generally can be defined as areas with endemic species. These areas are hierarchical in organization (thus a large area of endemism may contain smaller areas of endemism). To some (e.g. Crisci *et al.*, 2003), areas of endemism are naturally existing fundamental units of study for biogeographical explanation, and to others (e.g. Hovenkamp, 1997) they may not even be natural entities. The implications of these opposing views differ, so trying to understand areas of endemism in an ontological sense may help us to understand these implications more fully.

In the heat of the debate surrounding the 'species as individuals' thesis, Ghiselin (1980, p. 81) extended an ontological hand to biogeography when he suggested that 'Ranges, territories, and ecological niches are obviously individuals too'.

Ghiselin noted that continental fragmentation resembles lineage production and he hoped that biogeographical units would not be affected by the same philosophical blunders as surround species, for example considering them as classes.

Ghiselin's (1980) comments have largely been ignored through three decades of biogeographical discourse. Numerous authors have expounded on areas of endemism in terms of definition and discovery operations (e.g. Platnick & Nelson, 1984; Axelius, 1991; Platnick, 1991; Anderson, 1994; Harold & Mooi, 1994; Morrone, 1994; Riddle, 1998; Linder, 2001; Hausdorf, 2002; Szumik & Goloboff, 2004; Riddle & Hafner, 2006) but none have addressed the contribution of Ghiselin (1980) or alternative ideas (e.g. Hovenkamp, 1997; but see Hausdorf, 2002).

Craw (1983, p. 435) indicated operational and philosophical flaws with the way in which vicariance biogeographers used areas of endemism as their basic units:

The static de Candolle concept of an area of endemism as a natural biogeographic region has been adopted as the initial and 'unproblematical' unit in vicariance cladistics analysis. It is replaced in panbiogeographic analysis by the dynamic concept of these areas as constituting biogeographic boundaries. The basic units of vicariance cladistics analysis are not natural taxa, areas of endemism being neither *individuals* nor *historical groups* but biogeographic and geologic paraphyletic and polyphyletic groupings or *classes* as demonstrated below and by Craw (1983).

The main problem exposed by Craw (1982, 1983) was that these areas of endemism were often composite areas with reticulated, non-monophyletic histories.

The purpose of this essay is to make an ontological argument for areas of endemism as individuals and as real, naturally occurring entities (i.e. entities that exist without the necessity of human recognition) and to discuss the consequences of such a conclusion. The critical first step for the argument of areas of endemism as individuals is the recognition of species as individuals. The species-concept literature is replete with discussions of species as individuals (e.g. Hennig, 1966; Ghiselin, 1974, 1981, 1987; Hull, 1976; Wiley, 1980; Bernier, 1984; Holsinger, 1984; Kitcher, 1984; Mishler & Brandon, 1987; Ereshefsky, 1992; Frost & Kluge, 1994; Baum, 1998; de Queiroz, 1999; Coleman & Wiley, 2001; Mayden, 2002; Brogaard, 2004; Rieppel, 2007; Reydon, 2009).

The importance of these ontological discussions is that they provide a foundation for understanding species within evolutionary theory as well as for operational methods of species discovery. Recognition of areas of endemism as individuals would provide a similar foundation for framing questions in biogeography and evolutionary theory. For our argument we must assume that species are individuals, and *if species are individuals this lends credence to the proposition that areas of endemism are also individuals*.

There are a number of criteria necessary for an entity to be considered an individual (e.g. Strawson, 1959; Ghiselin, 1974, 1987; Mishler & Brandon, 1987; Frost & Kluge, 1994). First, it must be a particular thing, and second, there cannot be instances of it. Third, an individual is defined ostensively, not intensionally. The fourth criterion is that individuals have boundaries (which can be fuzzy) in space and time. A fifth criterion may be that individuals experience cohesiveness in their response to change. Baum (1998, p. 642) chose not to follow the path of Ghiselin and advocated a 'bottom-up' criterion that would allow, as he put it, 'a one-sentence definition of individuality', writing that an individual is 'a group of parts (entities at a lower hierarchical level) that, at a point in time, are more tightly connected to one another than to any entities (potential parts) that are outside the individual' (emphasis his). To some workers, it is not the idea of areas of endemism as individuals that is of interest, but rather what type of individuals they are: replicators, interactors, or replicator continua. Each of the above criteria is expounded below with regard to areas of endemism.

AREAS OF ENDEMISM AS INDIVIDUALS

Particulars and instances

Jamaica, Lake Tanganyika, Lower Central America are all examples of individual entities. The Blue Mountains are not a Jamaica, and neither is the Caribbean Sea nor the Cockpit Country. There are no things that can be considered instances of Jamaica, or for that matter of Lake Tanganyika or Lower Central America. Jamaica as an area of endemism is made up

of parts, both physical, for example the Blue Mountains and the Hellshire Hills, and biological, namely unique species. These parts form the thing Jamaica, but they are not Jamaricas. Areas themselves are individuals, and this acknowledgement plays an important role in our concept of an area of endemism. Ghiselin (1980, p. 81) said it best: 'If anything in the universe is an individual then a continent must be.'

Definition: intension or ostension

Areas of endemism are not intensionally defined: there is no list of specific characteristics that will always define areas of endemism. *Norops garmani* (a species of lizard) allows one to point to Jamaica and say that it is an area of endemism, but *N. garmani* diagnoses no other area. The same can be said for lemurs and Madagascar, for humans on Earth (as far as we know), etc. As such, areas of endemism are ostensively defined. They are diagnosable and can be diagnosed by the presence of species. Theoretically then, because of the hierarchical nature of endemism (infinitesimal areas have no unique species and the planet Earth has all unique species), an area of endemism can be diagnosed by the distribution of a single species. Humphries & Parenti (1999) also argued that one species was required to identify an area of endemism, whereas Platnick (1991), Harold & Mooi (1994) and Linder (2001) stated that a minimum of two species was necessary. Importantly, Riddle (1998) pointed out that under the definition of Harold & Mooi (1994) sympatry was not a requirement, and thus revealed the hierarchical nature of areas of endemism and opened the door for considering a single taxon as diagnostic. The argument for two species was based on the notion that without two taxa, there can be no discovery of repeated patterns. While that may be true, as far as the ontology of areas of endemism is concerned, every species above one simply adds to the diagnosis of the area of endemism.

It may also be possible to identify areas of endemism even when no unique species occur in an area, but instead when there is a unique combination of species. This is basically what Axelius (1991) proposed in her approach to identifying areas of endemism when there is overlap of areas. Linder (2001, p. 893) considered this conclusion an 'absurd situation of delimiting areas of endemism that lack endemic species'. However, when an individual cannot be independently diagnosed, it may be identified in relative terms, by a description that uniquely compares it with different individuals that can be independently diagnosed (Strawson, 1959). This is analogous to the description of a new species that is diagnosed by a unique combination of characters and not by the presence of a unique character. It is worth contemplating how such an area of endemism can come into existence. Two possibilities (there are probably more) come to mind (Fig. 1). First, consider a new vicariance event. The taxa in the newly separated areas would be a subset of the taxa from the formerly contiguous area, with partial overlap of taxa of these ex-contiguous areas. Prior to speciation, the newly vicariated areas would exhibit unique combinations of taxa, but no unique taxa. Another case

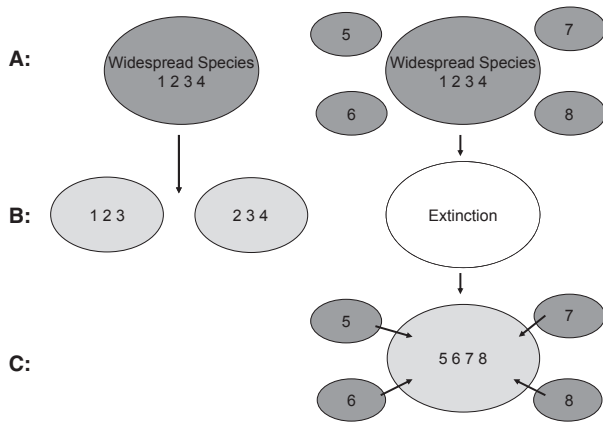


Figure 1 Schematic diagram depicting two possible formation processes that give rise to areas of endemism with unique combinations of species. Shaded areas indicate areas of endemism and differently shaded areas indicate different areas of endemism. Row labels A, B and C indicate temporal stages, and numbers represent a single species label (i.e. 1 = species no. 1). One process (left) involves a vicariance event that splits an area with species 1, 2, 3 and 4 into two new areas with unique combinations of species. The other (right) illustrates extinction in an area of endemism followed by recolonization via dispersal from surrounding areas. The recolonization results in a unique species assemblage and a new area of endemism.

would be an area that has experienced mass extinction. Dispersal from the surrounding areas would lead to the development of a mix of species, and this mix would remain until divergence of the lineages. Again, prior to speciation the area would consist of a unique combination of species with no unique species. Both of these possibilities are temporally bound ephemeral situations, but discoverable nonetheless.

Boundaries

The diagnosis of areas of endemism represents snapshots in time. Speciation, extinction, dispersion, dispersal, and the dynamic nature of the lithosphere are all reasons why areas of endemism have fuzzy boundaries in time and space. Speciation and extinction events alter the temporal boundaries. Speciation may bring an area of endemism into existence, and extinction may terminate its existence. Dispersion and dispersal alter the spatial boundaries. An area of endemism, pre-extinction, inhabited by species A, B and C is a different area of endemism from the same area inhabited by species D, E and F after extinction. Unlike the aforementioned processes, geographical and geomorphological dynamics can alter both spatial and temporal boundaries. Intuitively, then, it follows that tectonic fragmentation and accretion events affect the spatial and temporal existence of areas of endemism. Clearly, these entities are temporally ephemeral with beginnings and endings. Spatial boundaries of areas of endemism must also be blurry, making identification of the edges of areas of endemism difficult. Islands may seem like an exception to fuzzy spatial

boundaries, but that is dependent upon the snapshot in time. Early in the history of the island we now call Jamaica, it may have been fused to the south-eastern margin of the Yucatan (e.g. Pindell & Kennan, 2009). Subsequent to the translation of Jamaica away from the continent and into the Caribbean, the new island became submerged for millions of years and became subaerial c. 30–20 Ma (Crother & Guyer, 1996 and references therein). Even though the current spatial boundaries of the area Jamaica appear discrete, viewing the boundaries across time illustrates the blurred nature of the edges. In fact, pre-submerged Jamaica would be a different area of endemism from post-submerged Jamaica. All this indicates that these particular entities, areas of endemism, are not at all static but are dynamic (as per Craw, 1983).

Cohesion

The parts of a cohesive individual may respond to change in similar ways. If species are parts of an area of endemism, in what regard can this criterion be fulfilled? As previously noted, numerous factors are involved in the evolution and extinction of areas of endemism, but as an example we will use degree of isolation to discuss the point of cohesion. A continuous biota is fragmented, leading to isolation of a part of that biota. The species that compose that isolated biota, if severed from gene flow with the remaining biota, will, to varying degrees, respond to the isolation by beginning to track a unique evolutionary trajectory (each taxon diverges relative to the biota it is isolated from, i.e. speciation occurs). Consider the end of isolation or the loss of a physical barrier. The biota will respond to the end of isolation through expansion of their geographical ranges (to varying degrees). The cohesive response of species to isolation and loss of isolation is critical to the temporal and spatial edges of an area of endemism. Although Hausdorf (2002) did not use the term ‘cohesion’ in his description of the development of an area of endemism, he detailed a cohesive response of the biota to a vicariant event. Baum’s (1998) definition of individuality seems to be a form of cohesion and also lends credence to areas of endemism as individuals. It is easy to imagine an area of endemism as ‘a group of parts’ (parts = species, area) that ‘at a point in time are more tightly connected to one another than to any entities (potential parts) that are outside the individual’. For example, *Norops garmani* and *N. grahami* (Jamaica only) are currently more geographically connected to each other than either is to *Anolis carolinensis* (south-eastern North America).

Mereological sums

Another view of individuality, similar to Baum’s, says that individuals are mereological sums. That is, individuals are composed of parts that are themselves individuals (Brogaard, 2004). If the parts are individuals, then the whole is also an individual because the whole is nothing more than the sum of its parts. If the parts do not exist, the whole also does not exist. For areas of endemism the relationship to mereological sums is

obvious. Species and the area they are in are the parts, and species and the area they are in are individuals. The area of endemism is the whole and its parts are individuals. Because the whole is nothing more than its parts, an area of endemism is an individual. Furthermore, most obviously, if there are no species or an area (parts), there is no area of endemism (whole). Although it is not our intention to explore mereological sums deeply, if we followed Brogaard (2004) further, we would conclude that areas of endemism are more than simple mereological sums, actually being a specific kind of sum set apart from other possible sums by specific criteria. For now, we are satisfied that mereological sums provide an additional argument to the thesis that areas of endemism are not classes, but individuals.

Replicators, interactors and replicator continua

For biologists who view the individuality of areas of endemism as trivial it is more important to identify the *type* of individual in question. Entities varying in dynamic nature and coherence (meaning cohesive participation in processes) exist independently of human perception. The *interactor* type of individual is 'any entity that has the integration to undergo some unitary process' (Frost & Kluge, 1994) and must exhibit coherence. Areas of endemism are interactors in the physical process of plate tectonics, continental fragmentation and biotic dynamics (dispersal, range expansion and contraction, and speciation, extinction). *Replicators* are entities that 'pass on their structure largely intact in successive replications' (Hull, 1988, p. 408). A lineage, as defined by Hull (1988), is replication that results in the temporal persistence of an entity in the same or altered state [similar to Lidén's (1990) *replicator continuum*]. Areas of endemism do not exhibit the dynamics of replicators or the tokogenetic coherence of a lineage. They persist, via a lithosphere–biosphere coherence, as interactors, extinguished by biological dynamics (in this case extinction) or continental alterations. Similarly, they arise from the same processes, namely continental alterations and biological dynamics (speciation, dispersal, etc.). That is, areas of endemism can evolve, and thus are clearly not classes.

Hierarchical entities and the importance of scale

The hierarchical nature of areas of endemism can potentially present problems in the eyes of the operational biogeographer. Because areas of endemism can, and do, encompass numerous other areas of endemism, any area has the potential to be an area of endemism as the scale changes from less inclusive to more inclusive. It is only natural, then, for the practising biologist to question the functionality of areas of endemism and prematurely dismiss their use as the fundamental unit of historical biogeography.

The acknowledgement that species and areas of endemism are different kinds of entities is necessary and in no way promotes the dismissal of areas of endemism as the fundamental unit of biogeography. Frost & Kluge (1994) presented

two types of particulars, namely specification hierarchies and scalar hierarchies. Scalar hierarchies possess 'nontransitive boundaries that delimit levels' (p. 265). Such particulars 'are of importance to explanatory and process theories' (p. 265). While both species and areas of endemism are scalar hierarchical individuals by the definition of Frost & Kluge (1994), areas of endemism are different in that they are scale-specific in operation. In essence, species are irreducible in the study of species relationships. For example, if we take single organisms from several species and infer relationships, we are not inferring the relationships of those organisms but we are using those organisms as exemplars of the species, that is, as parts of a whole. In contrast, a biogeographer interested in the historical biogeography of the Caribbean Basin may utilize Jamaica and Hispaniola as areas of endemism. In a study of a different scale focusing on the biogeography of Jamaica, it is perfectly functional and operationally useful to diagnose and utilize new areas of endemism, such as the Blue Mountains, not used in the Caribbean Basin study. Hispaniola as an area of endemism can be reduced to the areas southern Hispaniola and northern Hispaniola, and the northern area could be reduced further. If we were interested in the historical biogeography of Hispaniola we could identify areas of endemism at a different scale than if we were studying the Western Hemisphere. Areas of endemism as scalar hierarchies are like Russian nesting dolls, in that a less inclusive area fits within a more inclusive area, but species are not, because one species does not fit within another, and they are equal in scale (contra de Queiroz, 2005). This is a significant difference between species and areas of endemism as individuals.

The concept

In summary, how do we conceive of an area of endemism? An area of endemism is a spatially and temporally bounded geographical area with species. Neither species alone nor geographical areas alone are sufficient for diagnosis. Species and the areas they are distributed in constitute a single unit. The space and time boundaries of these areas are flexible, as is their existence, because the species and the geographical areas themselves are interactors, involved in processes that can eradicate, shrink, or expand the areas of endemism. They are also reducible in that they are nested within one another. Operationally, an area that contains at least one unique species, or a unique combination of species, is an area of endemism, and the biogeographical use of multiple areas of endemism is scale-specific.

CONSEQUENCES

Strawson (1959, p. 37) wrote,

So the identification and distinction of places turn on the identification and distinction of things; and the identification and distinction of things turn, in part, on the identification and distinction of places.

If we replace 'places' with 'areas of endemism' and replace 'things' with 'species and area' we have a cogent statement about the diagnosis of areas of endemism by species and about an aspect of the diagnosis of evolutionary species through distribution. Species are required for the diagnosis of areas of endemism; therefore, an understanding of events alone is not sufficient for understanding the history of the distribution of biotas. Part of the diagnosis of evolutionary species (e.g. Simpson, 1961; Wiley, 1978, 1981; Frost & Kluge, 1994; de Queiroz, 1999) refers to the use of allopatry as an indicator, or as data for hypothesizing diagnosable lineages (e.g. Frost & Hillis, 1990; for an empirical example see Collins, 1991).

Opposition to the recognition of areas of endemism as real entities came from Hovenkamp (1997), who thought that areas of endemism did not exist naturally and perhaps were an unimportant question in historical biogeography:

As yet, there is no corresponding general theory of biogeography which predicts the existence of 'areas of endemism' which are characterized by taxa. It is even doubtful whether we have sufficient observations that support the existence of such areas.

(Hovenkamp, 1997, p. 68)

The claims of Hovenkamp (1997) are provocative. The recognition of areas of endemism as natural, particular entities is necessary and justified for the discipline of historical biogeography. What is the fundamental unit of biogeographical research? Vicariance events or areas of endemism? Given that biogeographical research concerns the biosphere as well as the lithosphere, it is intuitive and favourable to include a biotic element in this fundamental unit. Granted, if Hovenkamp (1997) is correct then something other than areas of endemism would need to be developed as this fundamental unit. Assuming that the argument for individuality holds, areas of endemism are indeed an appropriate unit of historical biogeographical inference and are fundamentally important in biogeographical and evolutionary processes as interactors. The current trend to develop event-based methods to the exclusion of areas of endemism, and thus the biota, while potentially enlightening about the history of areas says little about the history of the biota. Geophysical data represent only part of the information necessary to understand the history of areas and biota. Biological data may contradict geophysical hypotheses and provide the framework for developing novel geophysical hypotheses (e.g. Rosen, 1985). We believe that Crisci *et al.* (2003, p. 29) were correct when they wrote,

The concept of the area of endemism is controversial. It is subject to discussions from the most diverse perspectives, but at the same time *it is a central topic in historical biogeography*. It may be expected that in the future these discussions will clarify this concept, which *represents the natural unit of historical biogeography*. [italics ours]

As a matter of course, areas of endemism should never be assumed but be subject to discovery. On this matter we strongly agree with Hovenkamp (1997).

Hausdorf (2002) questioned the ideas of Hovenkamp (1997), and argued that Hovenkamp's approach does not

escape the problem of delimiting areas of endemism when there are overlapping distributions. Hausdorf (2002) saw the delimitation of areas of endemism as the major problem in using such areas as units of biogeographical study. He offered an alternative unit, the biotic element, which he defined as any group of taxa with distributions more similar to each other than to other groups of taxa. A question was left open: how many taxa make a group in the delimitation process of a biotic element? Interestingly, the claim is made (Hausdorf, 2002, p. 651) that, 'in contrast to areas of endemism, biotic elements can be determined by using distribution data alone'. We find this interesting because Hausdorf noted that 'the standard definition of an area of endemism is based on distribution patterns of species'. We do not see any difference between biotic elements and areas of endemism in terms of how they *should* be determined. We also disagree that such units are not historical in nature. Philosophically, we see all areas of endemism explicitly as historical entities, not just those considered as byproducts of vicariance.

Parsimony analysis of endemism (PAE) and other grid-based methods, when used with quadrats as areas (e.g. Rosen, 1988; Morrone, 1994; Crisci *et al.*, 2003; Szumik & Goloboff, 2004), are difficult to reconcile with the view that areas of endemism are individuals. As already discussed, it seems clear that spatial boundaries of areas of endemism are dynamic, and therefore fuzzy. Attempts to discover these areas via arbitrary grid boundaries cannot be successful. However, these methods have potentially powerful operational value and can provide first estimates for places to search for diagnosable areas. The relationship between PAE and ontological areas of endemism is similar to the relationship between the phylogenetic species concept and the evolutionary species concept: PAE is an operational concept that helps in the discovery of areas of endemism in the same way that the phylogenetic species concept helps in the discovery of species as framed by the evolutionary species concept (Frost & Kluge, 1994). We acknowledge that both operational concepts fall short in their ability to discover all possibilities covered under the philosophical concepts.

An understanding of areas of endemism similar to that of species, recognizing them as real, natural entities, is critical for the continued conceptual and empirical development of conservation biogeography. If all biotic distribution and its understanding is event-based, then in the absence of areas of endemism how do we begin to understand biodiversity hotspots? Are they just simple typological, static points? And if they (biodiversity hotspots) are recognized as such, how do discovery and management practices differ for them when they are viewed as dynamic systems that have fuzzy boundaries in time and space?

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