Title
Geology and climate drive diversification

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to replicate that effect perhaps underscores previously suggested[2,3] flaws in the blinding of earlier studies.

So what might be going on in these birds? Several other external stimuli that stop animals from responding to geomagnetic cues have been identified. Early studies of animal navigation noted that cues from the Sun or stars would take precedence over magnetic cues, leading to the idea that magnetism is the compass of last resort. It was then noticed that robins would ignore the magnetic field when the background intensity was shifted 20–30% outside the normal value[1], and that pigeons raced poorly during geomagnetic storms. From an evolutionary perspective, ignoring geomagnetic cues at such times makes sense, because anomalies in the background field are often associated with iron deposits or lightning strikes. Some animals also stop using their magnetic compass in the presence of red-only light, but such light is present only at sunrise and sunset, when the Sun compass is most reliable[3].

Hence, radio-frequency noise might be just another cue that tells migrating animals to ignore their magnetic sense, but the puzzle is why this might have evolved. Surprisingly, there is a natural source of the radio-frequency electromagnetic noise identified as disruptive by Engels and colleagues — that produced by solar storms. Coronal mass ejection (CME) events from the Sun slam plasma into Earth's magnetosphere every now and then, causing it to 'sing' at frequencies from as low as around 20 kHz up to the MHz range[7], some of which even leaks through Earth's normally radio-opaque ionosphere; the lower end of this range is remarkably close to that identified by the authors. These CME events generate the beautiful polar auroras, disrupt our use of the medium-wave radio band, and sometimes perturb the background geomagnetic field at Earth's surface enough to disturb animal navigation.

All known sensory systems in animals are based on cells specialized to convert the stimulus of interest into a coded stream of action potentials that are sent to the brain[8]. If the effects of radio-frequency radiation are real, such cells must exist, but the mystery is in the biophysics. The lack of an enhanced effect at the Larmor frequency, and the low levels of radiation concerned, make it unlikely that a previously proposed mechanism[6] for radio-sensing, based on light activation of a cellular protein called cryptochrome, is involved. But some magnetic effects on animals (such as that of a short, sharp magnetic pulse[1]) function through biological magnetite (Fe_3O_4) in tissue — might this also be the radio-wave detector?

If it is, how could such a detection mechanism have arisen? Early animals that had a simple compass patterned along the lines of magnetotactic bacteria would have needed to survive geomagnetic excursions or reversals — periods in which Earth's magnetic field weakened — and natural selection would have favoured individuals with higher cellular volumes of magnetite[3,9]. When the field recovered, animals would have been left with cells that have surprisingly large magnetic moments[9] (Fig. 1). Such cells might then have evolved to serve other functions, such as intensity-based magnetic navigation systems, increasing the amount of magnetite further. With large enough volumes of metallically conductive magnetite in these cells, direct detection of the small electric and magnetic vectors of radio-frequency radiation might have emerged, as Engels and colleagues suggest.

Do the authors' findings have implications for humans? It seems that geomagnetic sensitivity dates back to an early ancestor of animals, and it is clearly present in many extant mammalian species. Human tissues also contain biological magnetite[10]. Many people claim to be bothered by radio transmissions, and some have even moved to live in radio-frequency 'quiet zones' around radio telescopes. Modern-day charlatans will undoubtedly seize on this study as an argument for banning the use of mobile phones, despite the different frequency bands involved. However, if the effect reported by the authors stands the acid test of reproducibility, we might consider gradually abandoning our use of this portion of the electromagnetic spectrum and implementing engineering approaches to minimize incidental low-frequency noise, to help migratory birds find their way. ■

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EVOLUTION

Geology and climate drive diversification

Data from the Galapagos Islands exemplify how geology and climate can interact to cause episodes of isolation and fusion of the biota across a landscape. Different scales of such cycles dictate varying mechanisms of species generation.

ROSEMARY G. GILLESPIE
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Writing in the *Journal of Biogeography*, Ali and Aitchison[1] examine geological and climatic events over the past 700,000 years, namely island ontogeny and shifting sea levels, and their effects on biodiversity in the Galapagos Islands. The authors propose a process that can be considered a general evolutionary mechanism: that the dynamics of isolation caused by geological and climatological processes plays a fundamental part in shaping diversity. Whether these processes promote or constrain species diversification, however, depends on the spatial (global, regional or local) and temporal (multimillion, multimillennial or multidecadal) scales and periodicity of isolation and coalescence.

Geological events have long been known to mould and shape biodiversity. A breakthrough in understanding the underlying mechanisms came with the recognition that ancient splitting of landmasses resulted in shared diversity. The concept of vicariance biogeography — the separation of a group of organisms by a geographical barrier — provided the means for rigorous hypothesis testing in a hitherto largely descriptive field. This established that vicariance resulting directly from geological events can cause diversification, such that geological history will be clearly reflected in the resulting biotic assemblages. The isolation created by ancient geological events is fundamental. Yet, what is given is frequently taken away — separate land masses can become connected and biotic assemblages reunited to various degrees. For example, the Great American

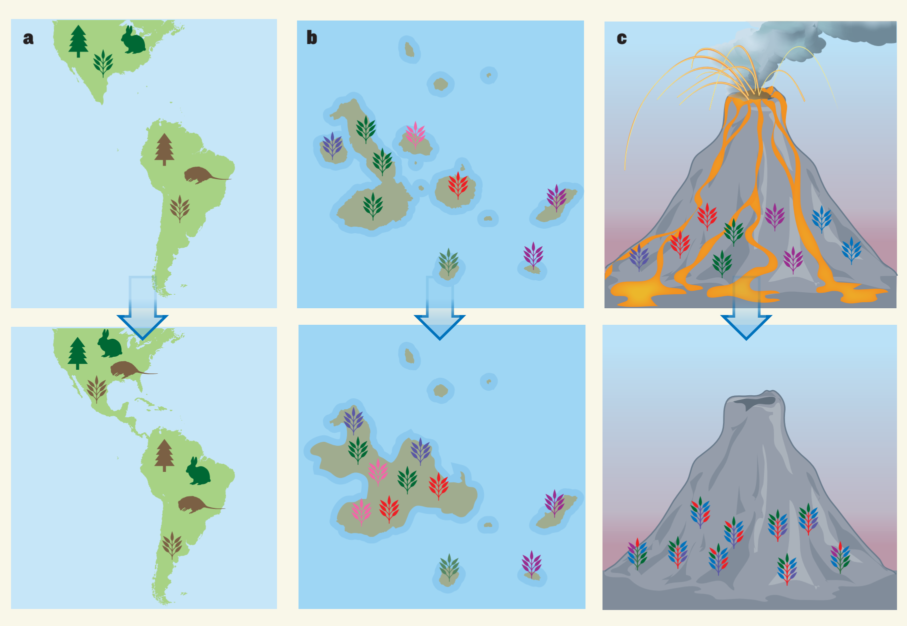

Figure 1 | Isolation across scales of space and time. a, On a multimillion-year timescale, distinct assemblages of biota form in isolation on different continents, and joining of the continents may lead to biotic exchange or species displacement. **b**, On a millennial timescale, different species may evolve in isolation on different islands; connections between these islands can then result in a richer biological assemblage as newly formed species come together. **c**, On a decadal timescale, populations may be isolated by recurrent events, such as volcanic eruptions; subsequent reconnection of these populations may result in new genetic combinations, a phenomenon that may also occur with invasive species.

Interchange associated with the formation of the Isthmus of Panama some 3 million years ago allowed the exchange of biotas of North and South America, each of which had evolved in isolation.

There is increasing evidence that geological and climatological events over shorter timescales (10,000 to 1 million years) and over smaller spatial scales (regional or local rather than global) can also influence the diversification process. A prime example of insights to emerge from such situations is provided by Ali and Aitchison in their model, which integrates the dynamics of geological and climatological events that repeatedly connected and disconnected islands of the Galapagos over the past 700,000 years. During this time period, these intermittent connections allowed otherwise landlocked vertebrates to disperse to other islands and to reconnect with populations that had previously been separated. More broadly, Ali and Aitchison use detailed palaeogeographical reconstructions to provide a series of explicit hypotheses about past population structuring and species formation that can be tested with molecular and geospatial data from extant species.

Although repeated separation and reuniting of biotas over a multimillennial time frame can obscure older geological and climatological events, the dynamics of geology and climate can be powerful forces in generating biodiversity. For example, work focused on time frames of 10,000 to 100,000 years ago has shown that climatological events can act as a 'species pump', in which periods of warming or drying serve to alternately isolate and reunite biotas. This phenomenon is well illustrated by Indonesian ants in the Sundaland rainforest, in which diversification has been attributed to repeated episodes of separation and connection of populations during the Plio-Pleistocene (around 5 million to 12,000 years ago), associated with fluctuating sea levels and climate[2]. Similar episodic isolation associated with climatic shifts has been inferred for the diversification of Amazonian vertebrates in the Pleistocene (around 2 million to 12,000 years ago)[3]. Even in the oceans, which have the potential for extensive mixing, opposing processes of isolation and exchange seem to have been responsible for much diversification[4].

On more recent (decadal) timescales and in localized areas, the same mechanism of isolation and mixing resulting from the combined effects of geological and climatological events can influence patterns of diversity prior to the formation of species. For example, population mixing and hybridization — resulting from previously separated populations coming back into contact — have had a key role in generating adaptive variation and functional novelty in populations of cichlid fish in African lakes[5]. Indeed, the repeated isolation and subsequent mixing of populations in new combinations may serve as an 'evolutionary crucible' to facilitate and potentially accelerate diversification[6]. Furthermore, the negative consequences of founder effects (the reduced genetic variation that occurs when a population is established by a small number of individuals) may be offset if different colonization events result in multiple genotypes within the introduced population. This process highlights the potential role of mixing among successively colonizing populations in providing the genetic variation to allow adaptive evolution[7].

Thus, geological and climatological dynamics over time and space shape the patterns of biodiversity that we can observe and measure today. Specifically, the periodicity of isolation and connection dictates evolutionary outcomes, and understanding of this dynamic has become the focus of genomic approaches[8]. When species evolve in isolation over long (multimillion-year) periods, reconnections can result in exchange or displacement of entire assemblages (Fig. 1a). When species are isolated for long enough to allow speciation (multimillennia), subsequent connections may unite newly formed species, thereby generating diversity (Fig. 1b). And when populations are isolated locally and over decadal timescales, thus prompting the development of disparate gene pools, subsequent reconnection and mixture can create new genetic combinations upon which selection can act (Fig. 1c).

Moving to the present and future, it is clear that, as organisms shift their distributions in response to climate change and as globalization increasingly homogenizes previously isolated biotas, understanding the role of historic isolation and recent connection in biodiversity dynamics is crucial. Indeed, the mixing of previously isolated populations is characteristic of many invasive species, suggesting a role for novel genetic combinations in their successful establishment in new environments. An increased knowledge of past events of isolation and fusion of biotas, such as that provided by Ali and Aitchison, will better equip us to predict future dynamics of biodiversity. ■

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