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Sonoric geography – addressing the silence of biogeography

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Executive Summary

In 2015, we called upon our colleagues to address a glaring oversight of a potentially transformative frontier in biogeography – the geography of sound (Lomolino et al. 2015). Our purpose here is to lay the conceptual foundations, based on the fundamental unifying principles of biogeography, to guide the development of the nascent field of **sonoric geography**. We define sonoric geography as an emerging subdiscipline of biogeography that attempts to discover and articulate patterns of geographic variation in the acoustic properties of biological communities and identify the underlying, causal explanations for those patterns.

We see at least two major benefits to this initiative. First, it will advance the field of biogeography by expanding the spectrum of biological properties studied – demonstrating how the field’s fundamental, unifying principles can be applied to a novel component of biological diversity – sound and acoustic assemblages across the principal geographic dimensions (area, isolation, elevation/depth, and latitude). Second, a research program in sonoric geography will, in synergism, advance the fields of soundscape ecology (Pijanowski et al. 2011, Slabbekoorn 2018) and acoustic ecology (Wrightson 2000) by integrating an explicit geographic context into their conceptual foundations, empirical investigations, and applications for conserving biological diversity, *sensu lato*—again, all this guided by the fundamental unifying principles of biogeography.

From fundamental principles to a conceptual model of sonoric geography

Biogeography’s fundamental, unifying principles

Despite the impressive and perhaps sometimes overwhelming diversity of patterns in the geography of nature we study, our attempts to articulate and understand the underlying causes for those patterns can be guided by a set of relatively simple, first principles (see Vellend 2010 for analogous efforts to synthesize theory and empirical patterns in community ecology). These principles can serve to better integrate and unify the broad spectrum of research programs comprising this, one of science’s most holistic and integrative disciplines. As the graphical, conceptual model of Figure 1 illustrates, the fundamental unifying principles

of biogeography assert that all patterns of geographic variation among biotas (species distributions, geographic variation in assemblages, etc.; central portion of the figure) result from:

- (1) non-random variation in environmental conditions across the geographic template;
- (2) the influence of those environmental conditions on the fundamental biogeographic processes of immigration (the arrival of species new to an area), extinction (the loss of a species from that area) and evolution (inclusive of speciation and microevolution), which in turn directly influence patterns in the geography of life (straight, blue arrows);
- (3) the influence of the fundamental processes on each other (e.g., evolutionary modifications of immigration abilities, or immigrations tending to ‘rescue’ otherwise isolated populations from extinctions) (black text and dashed lines); and
- (4) system feedback in the form of ecological interactions among species, which influence the fundamental capacities of other species to immigrate, survive, and evolve (green text and curved arrows in Figure 1).

Conceptual foundations of sonoric geography

In the first articulation of the fundamental, unifying principles of biogeography, Lomolino (2016) demonstrated their utility and applicability to a broad range of ecological and evolutionary patterns exhibited by insular biotas – primarily being patterns in species diversity and species composition, and morphological variation of island life across two geographic dimensions – island area and isolation. Here our focus is on the geography of sound, in general, and biophonies (sounds produced by organisms) in particular. A conceptual model of sonoric biogeography (Figure 2) is developed in parallel with that illustrated in Figure 1, based on the unifying principles of biogeography. Figure 2 proposes that the characteristics of acoustic assemblages (e.g. sonoric diversity and endemism – center of figure) result from:

- (a) non-random spatial variation in characteristics of the geographic template and, in particular, those of the **acoustic theater** (the combination of local,

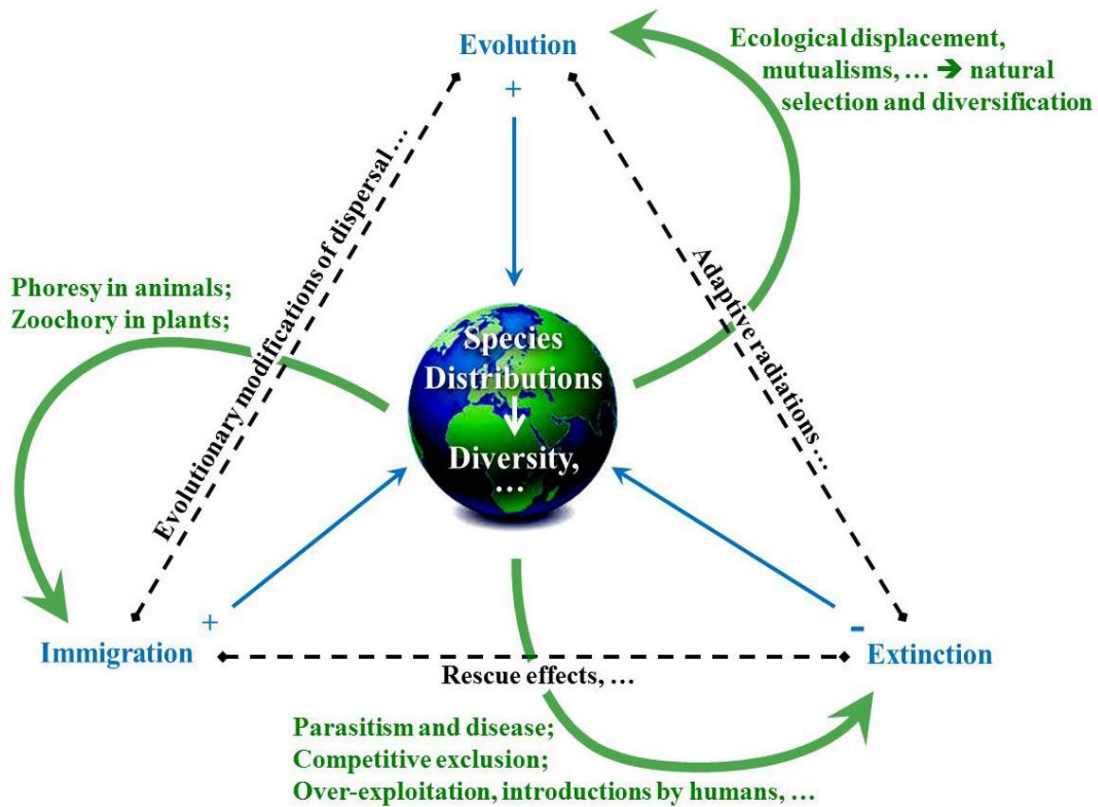


Figure 1. A graphical, conceptual model illustrating the fundamental, unifying principles of biogeography (Lomolino 2016; Lomolino et al. 2017).

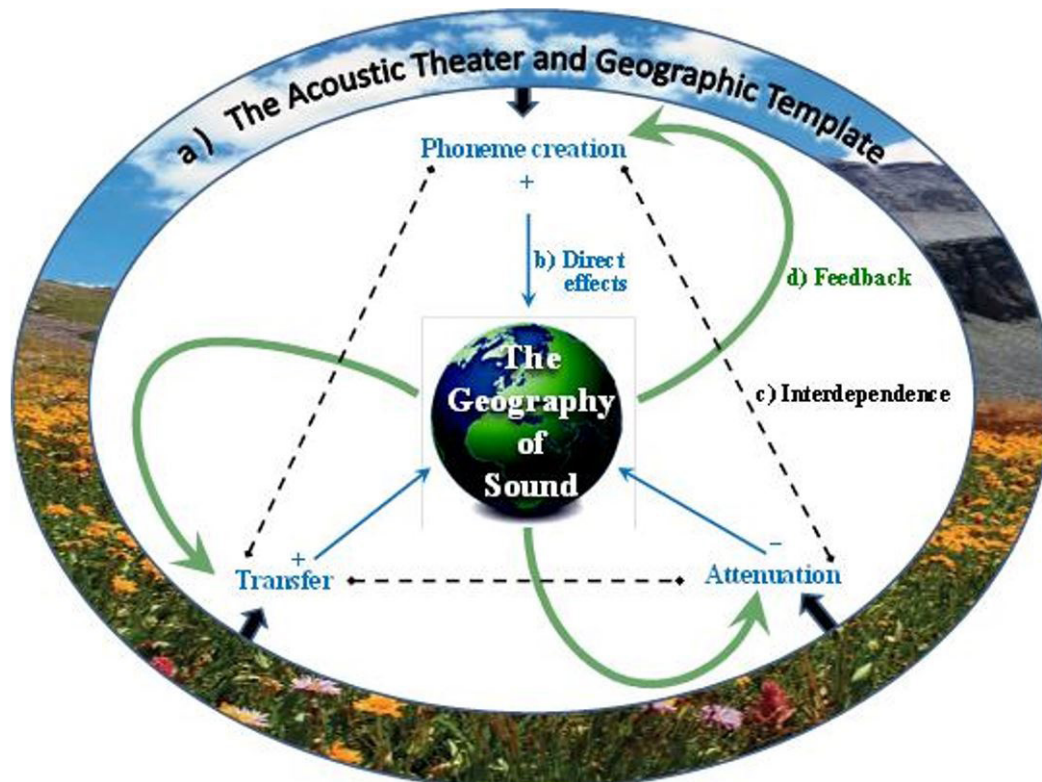


Figure 2. A graphical, conceptual model depicting the fundamental principles of sonoric geography. See text for explanation for (a) through (d).

- environmental features [e.g., plant formations, rocks, and water] that modify sound qualities),
- (b) the influences of that variation on the fundamental sonoric processes of phoneme creation, transfer and attenuation (i.e., the formation of new **phonemes** [perceptually distinct sounds analogous to cognate words], their transfer from one site to another, and their loss from local sites, respectively) – straight blue lines,
- (c) interdependence of these three, fundamental, sonoric processes (e.g., phoneme transfer to nearby sites creating a ‘rescue effect’ – reducing the likelihood of attenuation of that particular phoneme in the recipient site) – dashed black lines, and
- (d) sonoric system feedback, where sonoric characteristics of a local site or landscape influence the likelihood of phoneme creation, attenuation or transfer within that site, and to others as well – green curved lines.

Seminal research in sonoric geography

The long and distinguished history of research on sound has produced an impressive but burgeoning wealth of information – a grand legacy of data on the acoustic components of biological diversity (e.g., Marler 1955, Ryan and Brenowitz 1985, Endler 1992, Slabbekoorn and Smith 2002, Bradbury and Vehrencamp 2011). Yet, this impressive body of empirical data still lay wanting of a more integrative body of theory to explain and guide the advancement of these intriguing lines of research on the acoustic components of biological diversity and their patterns of spatial variation across the globe.

As we asserted elsewhere (e.g., Lomolino et al. 2017), just as Theodosius Dobzhansky argued that little in biology makes sense unless viewed in light of evolution, most if not all of the most intriguing features of biological diversity are rendered explicable when placed in a geographic context. Buffon’s¹ observations that different regions of the globe, even those with similar environmental conditions, are inhabited by distinct assemblages of species proved seminal to Darwin and Wallace’s theories of natural selection and, indeed, to the entire fields of biogeography, evolution and ecology. Thus, it may well be that the myriad of seemingly disarticulated acoustic phenomena may be interdependent and rendered explicable when analyzed through the microscope of a biogeographer: i.e., as patterns generated by a set of scale-dependent processes consistent with the persistent themes (Table 1) and the fundamental principles of biogeography – patterns that become emergent when visualized across the principal geographic dimensions of area, isolation, elevation/depth, and latitude.

We anticipate that current and future generations of biogeographers will discover a myriad of patterns in the geography of sound – genuinely novel insights that may be difficult if not impossible to predict in

these early stages of articulating a new subdiscipline of biogeography. It may, however, be fruitful to speculate on some likely research foci; in particular, those directly focusing on the nature of acoustic assemblages as they vary across the principal geographic dimensions.

- **Area:** Although the species–area relationship has been described as the closest thing to a rule in ecology, empirical patterns may be substantially more complex than the simple, canonical curve. We thus predict that various measures of acoustic diversity may, in parallel, exhibit a protean nature – taking on different forms (less dependent on area for smaller systems; log-linear, sigmoidal or even positive exponential on larger systems) depending on the scale-dependent processes influencing acoustic assemblages and how they vary in importance across a broad range of area.
- **Isolation:** As observed above, the effect of isolation on biological assemblages was indeed central to biogeography’s first law – Buffon’s Law, so it is likely that many future studies will assess distance-decay patterns of acoustic assemblages. Given possible convergent evolution in environmentally similar acoustic theaters (i.e., promoting sonoric convergence in similar biomes among the continents), we might anticipate that acoustic assemblages may exhibit multiple peaks of spatial autocorrelation (acoustic similarity), rather than continuous patterns of distance-decay as predicted by Buffon’s Law.
- **Elevation/Depth:** Biological diversity across the depths of the marine realm may be viewed as a continuation of those in elevation above the ocean’s surface and, indeed, the two gradients in species diversity above and below sea level appear to represent mirror images, at least in terms of their salient nature. A growing consensus of empirical studies on a broad diversity of plants and animals report a pattern where diversity peaks at an intermediate level; i.e., at points above and below sea level depending on the particular taxon, ecosystem and region studied. Similarly, given the non-random nature of spatial variation in the geographic template (which comprises the acoustic theater) and that the diversity of acoustic (biophonic) assemblages should be strongly influenced by the diversity of local biological assemblages, we predict intermediate peaks in acoustic diversity along gradients of elevation and depth.
- **Latitude:** Each of the geographic clines described above may be viewed in a hierarchical context, with patterns across distance, area or elevation, and depth nested within (varying among) more broad-scale patterns among latitudinal regions. Just as for other, anticipated patterns in acoustic assemblages, latitudinal gradients in acoustic diversity should be influenced by or reflect patterns in the character of the acoustic theater and of biological assemblages as well. Along with the physiognomic

¹ Georges-Louis Leclerc, Comte de Buffon, was a French naturalist (7 September 1707 – 16 April 1788)

Table 1. A sample of questions and research foci of sonoric geography that parallel the four persistent themes of biogeography (from Lomolino et al. 2017).

Biogeographic Themes	Soundscape Parallels/Questions
Classifying regions based on their biotas	Can soundscapes be similarly classified by their distinctive biophonies, and is there homogeneity within and distinguishing characteristics among sonoric regions analogous to that among biomes or biogeographic regions?
Reconstructing the historical development of lineages	Are there clear patterns of similarity of sonoric assemblages and acoustic communication (sound production and sensing) across lineages; e.g., such that the most closely related species have the most similar acoustic signals?
Explaining the differences in abundance and species richness among geographic regions	Do sonoric assemblages exhibit patterns in magnitude (volume) and acoustic diversity analogous to the broad-scale (latitudinal, elevational, etc.) patterns observed for biological assemblages?
Explaining geographic variation between populations and closely related species, including trends in morphology, physiology, behavior, genetics and demography	Does the acoustic composition of sonoric assemblages vary geographically consistent with characteristics of the acoustic theater, and with the morphological, physiological or demographic composition of the local animal communities?

or structural properties of regional biomes, climatic conditions along latitudinal gradients should alter resonance, early reflections, reverberation and attenuation of sound – key features of the acoustic theater. These may, in turn, shape which biophonies are produced, how they are transmitted across systems, and how some of those once novel to this system are lost. Given the anticipated acoustic phenomena of interdependence and feedback (points c and d in Figure 2), patterns emerging from the initial phase of research on sonoric geography may prove more complex, but we think far more interesting, than simple mimics of patterns in biological species diversity.

Applications for conserving biological diversity

Early on in the development of conservation biology as a rigorous, applied science, biogeography was recognized as a ‘cornerstone’ of the field (Wilson 1999). Accordingly, we anticipate that sonoric geographers will find numerous applications of their discoveries and seminal insights for conserving the diversity and native character of natural communities. Investigations into the above predicted patterns, along with a likely treasure trove of unanticipated gradients in acoustic assemblages, will prove essential for evaluating the efficacy of various measures of acoustic diversity as surrogates of species diversity. Rather than serving as simple correlates of species diversity, however, it is more likely that the first generation of sonoric

geography research will provide a toolkit of predictive models utilizing an eclectic suite of environmental parameters and relational formulae – all this based on empirical patterns discovered across the full suite of geographic dimensions.

Finally, as our colleagues in the applied fields have often emphasized, conservation biology is a value-laden science. To this point, we return to a central assertion of our original paper on *The Silence of Biogeography* to emphasize that *sound* is an integral component of biological diversity and the distinctiveness of place. With each of the thousands of species extinctions that occurred during the late-Pleistocene and early-Holocene, a marvelous cacophony of the chorus of nature was lost, along with an incalculable measure of distinctiveness of place (biogeography’s most fundamental pattern). The persisting native sounds of the natural world are precious elements of biological diversity worthy of conserving on their own merit. And so we call on our colleagues to take on the challenges of exploring the geography of sound, articulating some of its most salient patterns, developing its seminal models, and applying all of this to prevent the threatened voices of the natural world from becoming just waning, faint echoes of life that once called, and chirped and sang across this planet.

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