

Toward a Mechanistic Understanding of Linguistic Diversity

Author(s): Michael C. Gavin , Carlos A. Botero , Claire Bowerman , Robert K. Colwell , Michael Dunn , Robert R. Dunn , Russell D. Gray , Kathryn R. Kirby , Joe McCarter , Adam Powell , Thiago F. Rangel , John R. Stepp , Michelle Trautwein , Jennifer L. Verdolin , and Gregor Yanega

Source: BioScience, 63(7):524-535. 2013.

Published By: American Institute of Biological Sciences

URL: <http://www.bioone.org/doi/full/10.1525/bio.2013.63.7.6>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Toward a Mechanistic Understanding of Linguistic Diversity

MICHAEL C. GAVIN, CARLOS A. BOTERO, CLAIRE BOWERN, ROBERT K. COLWELL, MICHAEL DUNN, ROBERT R. DUNN, RUSSELL D. GRAY, KATHRYN R. KIRBY, JOE McCARTER, ADAM POWELL, THIAGO F. RANGEL, JOHN R. STEPP, MICHELLE TRAUTWEIN, JENNIFER L. VERDOLIN, AND GREGOR YANEGA

Our species displays remarkable linguistic diversity. Although the uneven distribution of this diversity demands explanation, the drivers of these patterns have not been conclusively determined. We address this issue in two steps: First, we review previous empirical studies whose authors have suggested environmental, geographical, and sociocultural drivers of linguistic diversification. However, contradictory results and methodological variation make it difficult to draw general conclusions. Second, we outline a program for future research. We suggest that future analyses should account for interactions among causal factors, the lack of spatial and phylogenetic independence of the data, and transitory patterns. Recent analytical advances in biogeography and evolutionary biology, such as simulation modeling of diversity patterns, hold promise for testing four key mechanisms of language diversification proposed here: neutral change, population movement, contact, and selection. Future modeling approaches should also evaluate how the outcomes of these processes are influenced by demography, environmental heterogeneity, and time.

Keywords: linguistic diversity, biogeography and ecology, geographic patterns, research methods, languages

Explaining patterns of diversity is a central challenge of ecology and evolutionary biology. Thousands of studies (indeed, entire journals) have employed a well-developed set of methodological and theoretical tools to explain spatial patterns in biodiversity. This body of work has made important advances and has much to offer researchers interested in other types of diversity. We focus here on the ways in which advances in ecology and evolutionary biology can support the analysis of drivers of linguistic diversity. There is an astounding array of linguistic diversity. For example, the world's inhabitants speak nearly 7000 languages, patterned unevenly across the planet (figure 1). The island of New Guinea covers less than 0.5% of the Earth's land area yet supports over 900 languages (some 13% of all languages), whereas Russia has only 105 languages despite being 20 times larger. However, our knowledge of the drivers and mechanisms behind patterns of linguistic diversity is limited, despite the fundamental importance of the question for our understanding of human cultural evolution.

In this article, we seek to advance our ability to explain geographic patterns of linguistic diversity. We divide this task into two main parts: First, we review the small set of empirical studies whose authors have attempted to identify the drivers behind these patterns. Second, we outline

a program for future research on the topic by highlighting methodological and theoretical considerations for explaining patterns of linguistic diversity. In particular, we draw on previous empirical and theoretical work to outline the mechanisms that drive linguistic cladogenesis and disparity. We conclude the article by suggesting directions for future research in the field.

What is linguistic diversity?

Languages, like biological species, are related through nested patterns of descent, such that patterns of language diversity can be studied at different taxonomic levels. Languages also differ on a multitude of structural levels, including the organization of the sound system (phonology); systems for the combination of meaningful elements into words (morphology) and phrases (syntax); and systems for indicating space, time, speaker attitude, and epistemological status (e.g., eyewitness, common knowledge, hearsay).

We distinguish three types of language diversity. *Language richness* refers to the number of languages within a given area. *Phylogenetic language diversity*, following the definition used for *phylogenetic diversity* in evolutionary biology, is the minimum total length of all branches needed to span a set of taxa on a phylogenetic tree (Faith 1992). *Linguistic*

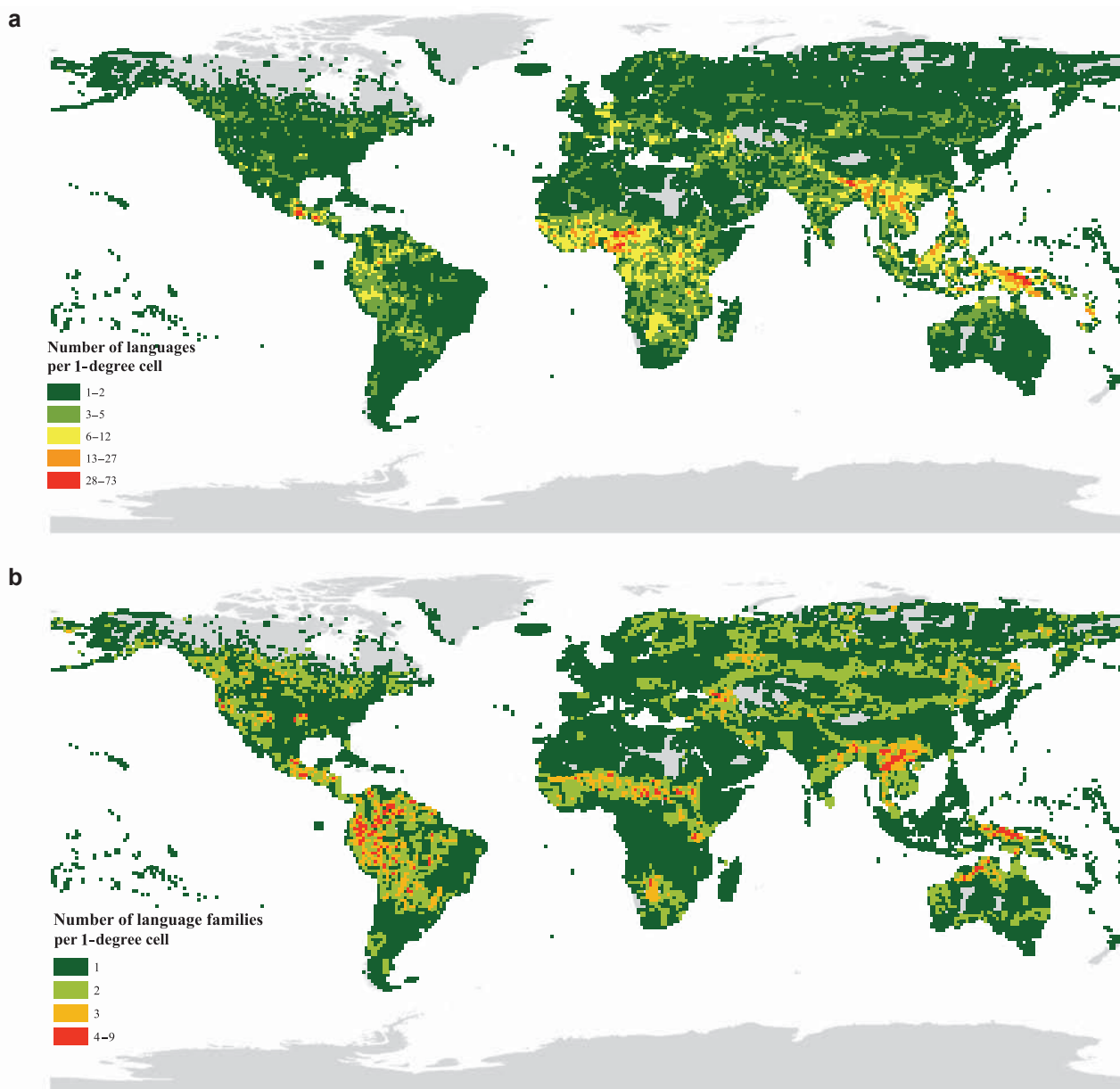


Figure 1. Global patterns of linguistic diversity as expressed by (a) the number of languages per 1-degree cell and (b) the number of language families per 1-degree cell. The size of cells used in the analysis for these studies was measured in degrees of latitude and longitude, such that a 1-degree cell spanned 1-degree latitude and 1-degree longitude. The data are from the World Language Mapping System (www.worldgeodatasets.com/language).

disparity refers to the range of expression in a language trait within a clade. Languages differ on a multitude of structural levels, including phonology, morphology, and syntax. Each of these types of language diversity reflects distinct geographic patterns (e.g., see figures 1 and 2). Note that language richness is generally the product of language-splitting events (cladogenesis), whereas phylogenetic diversity and disparity are produced by both anagenesis (change within lineages) and cladogenesis (figure 3). In the context of this article, the different aspects of linguistic diversity are not

necessarily distributed in the same way. For example, the number of language families present at a location is only moderately correlated with the number of languages (e.g., $r = .6$; figure 1).

Review of empirical studies of linguistic diversity

In the next section, we review the limited set ($n = 12$) of empirical studies that were designed to test the factors driving linguistic diversity. We found that the factors that have been identified to date as influencing the

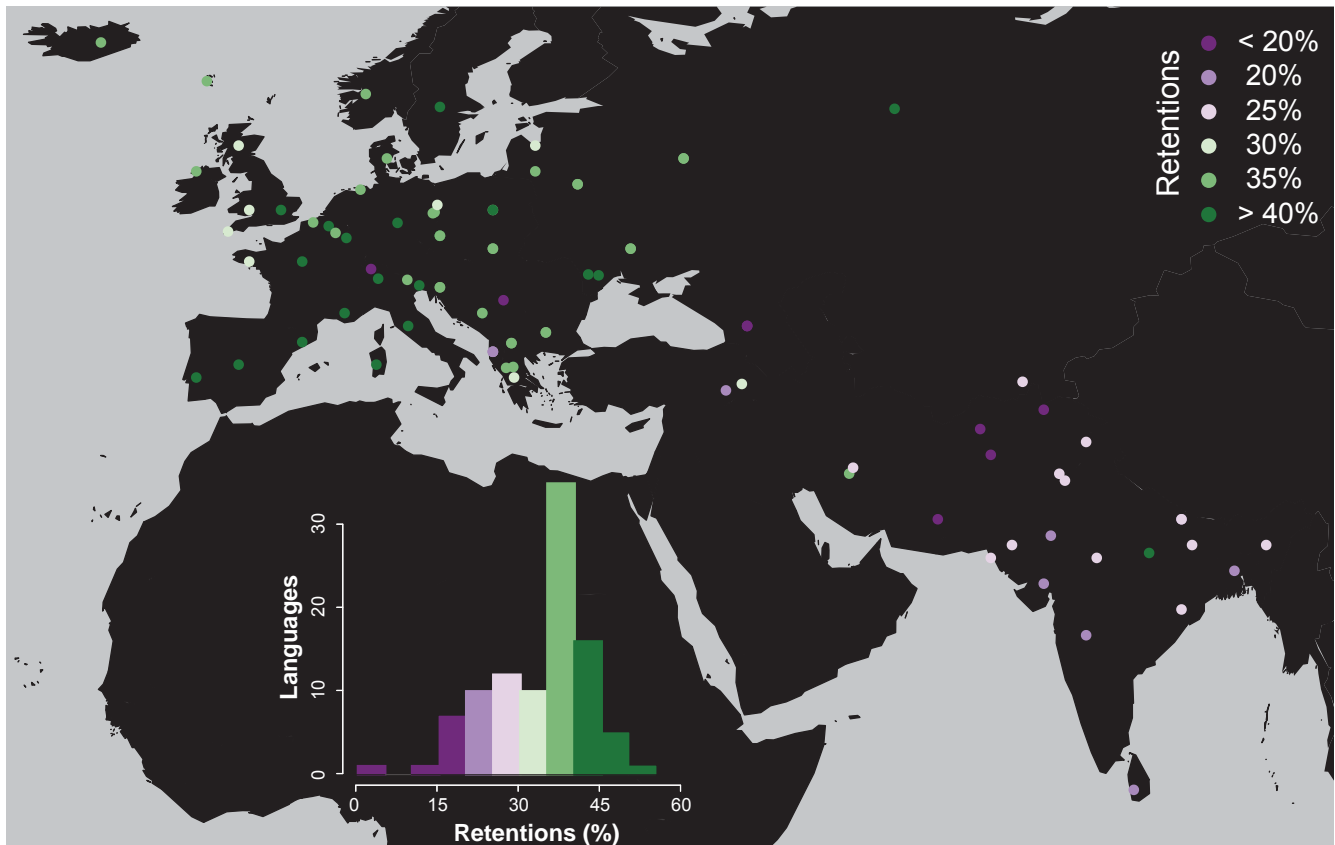


Figure 2. Language relationships can be inferred using evolutionary models of innovation and the loss of cognate forms (words that can be shown to descend from a common ancestor). To do this, linguists usually use some form of a Swadesh list, a standard list of meanings, which are relatively stable and widely shared. This figure shows the percentage of the Swadesh list that can be traced all the way back to the ancestral node of the Indo-European family tree, calculated for 98 Indo-European languages (the data are from Dunn and colleagues [2011]). Lexical diversity is generally higher in the eastern parts of the map.

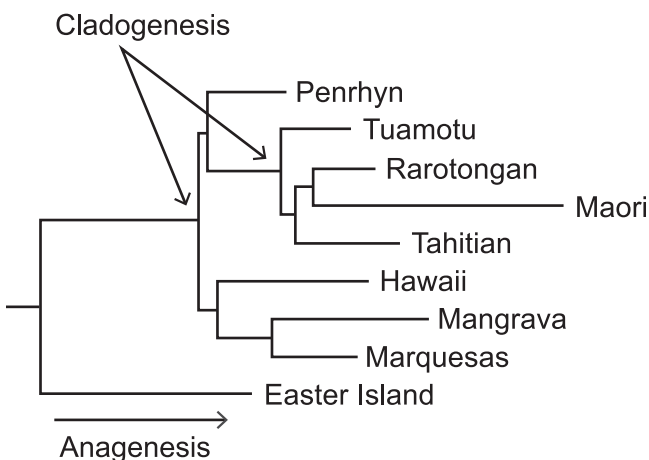


Figure 3. An example (from a subset of Polynesian languages) of two distinct processes shaping language diversity: language-splitting events (cladogenesis) and change within lineages (anagenesis).

geographical patterns of linguistic diversity fall into three broad categories: environmental, topographic, and socio-cultural (table 1). In general, all factors in these categories have been shown to influence linguistic diversity to some degree. However, although a few factors (e.g., net primary productivity) consistently show some influence across studies, there is limited agreement on many factors. For example, Nettle (1996, 1998, 1999a) found support for the role of mean growing season (MGS) in driving linguistic diversification, whereas others (e.g., Currie and Mace 2009) have emphasized a more limited role for environmental variables. We expand on these observations below.

Our review includes studies for which the dependent variable is the number of languages and studies in which language range size was examined. This is because the historical ranges covered by languages have rarely overlapped geographically—unlike species ranges in studies of geographical patterns of biodiversity. (Although the vast majority of language ranges still do not overlap, recent movements, including those to urban areas, have led to an increase in overlapping.) Because of this historical lack of

Table 1. Empirical studies in which measures of language diversity were investigated.

Study	Geographic area	Unit of analysis	Empirical approach	Dependent variable
Currie and Mace 2009	Old World ^a	Ethnolinguistic group	Linear mixed model	The area over which the language is spoken
Currie and Mace 2012	Global	Ethnolinguistic group	Hierarchical linear modeling	The area over which the language is spoken
Fincher and Thornhill 2008	Global	Country	Correlation	Language richness
Gavin and Sibanda 2012	Pacific Islands	Island	Multiple regression	Language richness
Mace and Pagel 1995	North America	Country	Correlation	Language density
Manne 2003	Central and South America	Cell (1°) ^d	Correlation, nonparametric regression tree analysis	Language richness
Michalopolous 2008	Virtual	Cell (0.5° × 0.5°), country	Multiple regression	Language richness
Moore et al. 2002	Sub-Saharan Africa	Cell (2° × 2°)	Multiple regression	Language richness
Nettle 1996	West Africa	Cell (2°)	Correlation	The number of languages per area and per head of population
Nettle 1998	Global ^b	Country	Correlation	The number of languages per area and per head of population
Nettle 1999a	Global ^c	Country	Correlation	Language diversity per area and per head of population
Sutherland 2003	Global	Country	General linear modeling, correlation	Language richness

^aThis sample excluded the Americas and Australia.

^bThis study included a global sample of 74 countries, restricted to tropical countries larger than 50,000 square kilometers and excluding those with a variable mean growing season (MGS).

^cThis global sample included an unspecified number of countries, restricted to tropical countries larger than 50,000 square kilometers and excluding those with variable MGS.

^dThe size of cells used in the analysis for these studies were measured in degrees of latitude and longitude, such that a 1-degree cell spanned 1-degree latitude and 1-degree longitude.

language overlap, a strong relationship exists between language richness within a given area and the average size of language ranges (i.e., more languages with small ranges can be found in a given area than languages with large ranges). In the studies included here, several different response variables have been used, such as the number of languages per country, the number of languages per map grid cell, and language range size.

We limited our review to studies in which the factors driving linguistic diversity were empirically examined. In doing so, we did not include a number of other studies in which the predictive power of specific variables was not explicitly assessed (e.g., Smith 2001, Loh and Harmon 2005, Gorenflo et al. 2012, Laitin et al. 2012) or that were focused on related concepts (such as ethnic diversity) but not explicitly on language (e.g., Birdsell 1953, Cashdan 2001). In general, the findings of these other studies corroborate those in table 1. For example, in a pioneering study, Birdsell (1953) showed the role of environmental productivity in influencing the distribution of ethnic groups.

Moreover, we limited our review to language diversity, not phylogenetic or family diversity. For one, we are aware of no studies in which an empirical examination was conducted

of the factors leading to geographical patterns in phylogenetic language diversity. No credible global language tree exists (Campbell and Poser 2008), and there are a limited number of examples of language trees with reliable estimates of time since divergence (e.g., branch length estimates for Austronesian; Gray et al. 2009). We also did not consider language family diversity because, as was noted by Nettle (1999a), different authors call different sets of groupings *families*, without a consistent definition of what constitutes a *language family*.

Environmental variables. Environmental variables, both climatic and ecological, have been noted as important predictors of linguistic diversity patterns in quantitative studies. Given the strong latitudinal gradient in language richness (see figure 1a), it is inevitable that many climatic variables correlate with language richness. Many mechanisms might explain such patterns. Nettle (1998, 1999a) hypothesized that shorter MGS (defined as the number of months with mean temperatures above 6 degrees Celsius and mean precipitation [in millimeters] at least double the mean temperature) contribute to greater ecological risk for humans, who in turn must increase social network size to cope with

the risk, which leads to linguistic homogenization. Nettle (1996, 1998, 1999a) found a robust and strong association between MGS and language diversity.

However, subsequent studies (table 1; Sutherland 2003, Currie and Mace 2009, Gavin and Sibanda 2012) in different regions have shown less support for the role of MGS. Given the latitudinal patterns present, it is surprising that previous studies have indicated that both individual environmental variables, such as net primary productivity, and suites of environmental factors explain (in the statistical sense) only a small percentage of the variance in linguistic diversity (e.g., less than 20%; Moore et al. 2002, Currie and Mace 2009). Recent work shows that the importance of environmental factors such as net primary productivity and MGS is likely to change over time and that there is a significantly greater influence of these factors in forager and pastoralist groups than in agriculturalist societies (Currie and Mace 2012).

In several previous studies, correlations have also been noted between linguistic diversity and biological diversity (e.g., bird diversity, Sutherland 2003; plant diversity, Stepp et al. 2004; mammal diversity, Sutherland 2003; disease diversity, Fincher and Thornhill 2008; biodiversity, Moore et al. 2002). Moore and colleagues (2002) reasoned that geographical patterns in biological and linguistic diversity may be associated through three possible avenues: (1) Biodiversity facilitates language diversity through resource partitioning, (2) similar social processes and technologies can erode both cultural and biological diversity, and (3) biological and language diversity respond in similar ways to environmental variables. However, all these studies were conducted at coarse global or regional scales, and the relationship between biological and language diversity is not always as strong when a finer filter is applied (e.g., within South America; Manne 2003). Moreover, this relationship is not necessarily mechanistic: Language diversity and biological diversity might simply respond to similar (or at least intercorrelated) drivers and constraints, rather than being associated with each other causally.

Spatial heterogeneity variables. Studies in biogeography have shown that more spatial heterogeneity, as measured by more-diverse habitats or higher topographic complexity, is often correlated with greater diversity (Kerr and Packer 1997). A link between spatial heterogeneity and diversity also appears to exist for languages. Both Michalopolous (2008) and Mace and Pagel (1995) noted strong correlations between habitat heterogeneity and linguistic diversity. Isolation, such as that created by mountains or oceans, is theorized to promote cultural and linguistic diversity by increasing the costs of social interaction with neighboring groups (Stepp et al. 2005), but the evidence for this effect is mixed. For example, Nettle (1996) noted a negative correlation between language range size and altitudinal variation ($r = -.60$, $p < .001$), whereas Currie and Mace (2009) concluded that topography (measured as the standard deviation

of altitude within a grid cell) has only a weak correlation with language range size at a global scale. Gavin and Sibanda (2012) found that more-isolated islands in the Pacific support less language diversity (possibly because of either the time since the last settlement or environmental factors that covary with isolation—e.g., soil fertility). Independent of an effect of barriers on isolation, different habitats may also lead to distinct livelihood strategies and the formation of ethnolinguistic boundaries.

Sociocultural variables. Over time, individual human populations may divide into new ethnolinguistic groups. It is likely that human languages reached their maximum number (estimated at 12,000) at the end of the Pleistocene, directly predating the rise of agriculture (Harrison 2007). In the hunter-gatherer societies of the time, the dominant force in language creation is likely to have been fissioning mechanisms, which resulted from a maximum group size of around 500–1000 individuals (Hamilton et al. 2007). The time since settlement does not, however, strongly correlate with linguistic diversity (Sutherland 2003, Gavin and Sibanda 2012). Indeed, the number of languages has been in decline since the Neolithic as agricultural groups have spread, replacing hunter-gatherers, and population movements have tended to reduce language stock diversity (Nettle 1999b).

Currie and Mace (2009) concluded that political complexity is a key driver of patterns in language range size, a result that supports a large body of theoretical work in which it is posited that the spread of politically complex agricultural societies is a dominant factor in the reduction of language diversity (Renfrew 1994). Other sociocultural factors, including relative wealth, social connectedness, and subsistence strategies, have garnered little support from previous empirical studies (Sutherland 2003, Fincher and Thornhill 2008, Currie and Mace 2009).

In summary, the studies outlined above have made some important advances in highlighting several key factors associated with the geographical patterns of language diversity. However, drawing universal conclusions from the literature is difficult, given the range of analytical approaches used, the different scales of analysis, the different focal locations (e.g., South America, Africa, Australia), and the sometimes-contradictory results (table 1; also see supplemental table S1, available online at <http://dx.doi.org/10.1525/bio.2013.63.7.6>).

Methodological considerations for future studies

In this section, we address key methodological and theoretical issues for the further study of linguistic diversification. We begin by outlining concerns and considerations for the methodologies used to tackle this complex problem, drawing on tools and techniques developed in studies of biological diversity. Next, we outline the theoretical issues that underlie the mechanisms of linguistic diversification.

Future work on the geographical patterns of linguistic diversity will need to take into account several methodological considerations. Fortunately, hundreds of studies have

been focused on the geographical patterns of biodiversity, and methodological advances in biogeography and macroecology can help guide future work on the patterns of linguistic diversity.

Undoubtedly, multiple factors shape the geographical patterns of diversity. Therefore, research must move beyond single-factor correlative studies, and multicausal approaches should be pursued through multivariate statistical methods. In recent years, several perils of such methods have been confronted and adequately resolved in the biodiversity and macroecology literature, offering a guide for the geographical analysis of language diversity. First, when environmental or other candidate predictor variables are correlated among themselves (a condition called *multicollinearity*), it becomes difficult to infer causality. Multicollinearity can be quantitatively assessed (e.g., with variance-inflation factors), and where significant problems exist, alternative avenues for analysis can be applied—for example, by combining raw variables through factor analysis or principal components analysis (PCA; Willig et al. 2003). Of the empirical studies reviewed here, PCA was used in three to combine predictor variables (Nettle 1996, Moore et al. 2002, Currie and Mace 2009), and Currie and Mace (2009) and Gavin and Sibanda (2012) tested specifically for multicollinearity.

Second, like biological diversity, language diversity demonstrates strong spatial patterns (see figure 1), and the environmental and social processes shaping language diversity (e.g., ecological risk and political complexity) are also spatially structured. When analyses are done on spatial-patterned variables using geographical-gridded data, adjacent or nearby grid cells tend to have values similar to those of these variables because of a common cause and are therefore not statistically independent (spatial autocorrelation). Unless spatial autocorrelation in model residuals is accounted for, sample sizes tend to be spuriously inflated, and relationships among variables may falsely appear statistically significant (a type I error). Several spatial modeling strategies are available to measure and account for the spatial autocorrelation in correlative studies (see Beale and colleagues [2010] and the references therein). For example, Moore and colleagues (2002) tested for spatial autocorrelation, and Gavin and Sibanda (2012) used spatially explicit models to explore the drivers of linguistic diversity patterns.

Third, because they often share historical roots of cultural evolution, related ethnolinguistic groups cannot be considered causally independent units, a statistical challenge referred to as *Galton's problem* or *phylogenetic autocorrelation* (Naroll 1965). As with species, more closely related sociolinguistic groups are more likely to live closer to each other than less closely related sociolinguistic groups and are also more likely to have similar mechanisms determining their geographical distribution that arise from shared history rather than from independent origins (Mace and Pagel 1995). Therefore, in order to ascertain the degree to which specific mechanisms drive geographical distributions in

languages, any shared history of the ethnolinguistic groups in question must be controlled for.

Several different statistical approaches have been used in biogeography and evolutionary biology studies to cope with phylogenetic autocorrelation, the most common of which has been the independent contrasts method (for a review of the advantages and disadvantages of this and related approaches, see Freckleton [2009]). To date, in no studies of language diversity have the levels of phylogenetic autocorrelation in the data been reported or controlled for. Instead, Galton's problem has been handled in three ways: It has been ignored, data have been separately analyzed by geographical region, and linear mixed models have been used. In a few studies (e.g., Nettle 1999a, Fincher and Thornhill 2008), separate analyses were conducted for different regions of the globe to account for geographical variation in the historical influences on language distributions. However, the regional divisions have been at a macroscale (e.g., Africa versus North America), which can obscure the differences in diversification mechanisms present at finer scales. In addition, this approach will not capture historical influences that are not geographically structured (Nettle 2009). Alternatively, for example, Currie and Mace (2009) included language family as a random effect in linear mixed models that predicted language diversity levels within map grid cells, whereas Currie and Mace (2012) used a hierarchical linear modeling procedure to the same effect. However, families are only one possible level of language classification. Recent advances in language phylogenetic analysis have led to more robust language trees for several language families (e.g., Austronesian; Gray et al. 2009), and more such studies are under way. Combining these new language trees with the use of random effects in linear mixed models, hierarchical linear modeling, or the independent contrasts methods can allow future analyses to capture in more detail the influence of phylogeny on language diversification patterns.

Fourth, multicausal explanations sometimes call for more complex statistical models. Previous statistical models have been focused almost exclusively on the direct causal pathways by which explanatory variables may influence language diversity; these pathways have been modeled as simple linear functions. However, not all explanatory variables can be expected to exhibit a strict linear relationship with language diversity. Exploring nonlinear functions with model selection techniques (e.g., Burnham and Anderson 2002) to avoid overfitting may increase the fit of some models of language diversity, an approach that has been tested in studies of species richness patterns (e.g., Willig et al. 2003). In addition, theory suggests that language diversity will be shaped by a complex web of causal factors (Currie and Mace 2012). For example, the development of grain-based agriculture in different temperature regimes around the world required the presence of particular environmental conditions and a source of potential cultivars. In some regions, agriculture supported the formation of larger and more politically complex societies, in which cultural traits, such

as language, tended to become standardized (Johnson and Earle 2000). In this case, the impact of environmental conditions on language diversity is not linear (e.g., agriculture is not well suited to extremes of temperature or precipitation) and is only indirect, because it is mediated through the influence of agriculture and political complexity. Structural equation modeling (SEM), a technique for modeling and assessing multiple hypotheses in causal networks, can help differentiate the direct and indirect influences of different causal factors. However, in the use of SEM, its limitations must be recognized—in particular, the dangers of a poorly designed model. For example, the omission of key variables or causal pathways can lead to biased parameter estimates and inaccurate standard error estimates (see Tomarken and Waller [2005] for a full review of the advantages and limitations of SEM). Currie and Mace (2009) used a simple three-variable SEM to examine the relationships among MGS, political complexity, and language range size; more-complex versions have the potential to provide a more complete picture of the web of causality shaping language diversity patterns.

The explanatory variables related to language diversity may well vary among geographical regions. Therefore, modeling approaches that explicitly account for spatial patterning in causal explanations (called *nonstationarity*; e.g., geographically weighted regression; Fotheringham et al. 2002) should be explored. To date, in none of the empirical studies of language diversity have analytical procedures that account for nonstationarity been used. Willig and colleagues (2003) highlighted two different attributes of scale that can influence the results of studies of diversity patterns: focus (the dimensions of the sampling units) and extent (i.e., geographical-space sampled). This conceptual framework may help explain why studies in which a different focus (e.g., countries or grid cells as the unit of analysis) or a different extent (e.g., global or continental) was used have reached different conclusions concerning the potential drivers of language diversity patterns.

Studies of linguistic diversity patterns must also grapple with the dynamic nature of diversification processes over time. Language diversity has developed and changed at variable rates over millennia, diversifying in punctuated bursts (Atkinson et al. 2008) related to fluxes in environmental and social conditions (Nettle 1999a, Pagel et al. 2007). To date, most models have used only current data on language diversity and its candidate predictors, but understanding the mechanisms behind language diversification will require incorporating temporal changes in the key factors influencing diversification. One way temporal changes could be investigated is to use recently developed Bayesian methods to model changes in diversification rates in language phylogenies (Currie and Mace 2012). For example, Gray and colleagues (2009) used this approach to locate changes in the diversification rate of a large phylogeny of Austronesian languages. They argued that the availability of appropriate social and technological resources probably determined the

timing and location of the four diversification pulses that their analyses were able to identify.

To date, models of linguistic diversity have also rested on the implicit assumption that language richness is spatially uniform in the absence of environmental, biological, or social gradients. In work on the middomain effect in biogeography, it has been concluded that if species' ranges are allowed to evolve randomly within a bounded geographical domain, the resulting model will produce a richness peak or plateau in the middle of the domain (the relevant literature was reviewed by Colwell and colleagues [2004]; also see Colwell and Rangel [2010] for a version of the model with invariant range sizes). However, in null models of species ranges, it is assumed that an unlimited number of species can be found in the same location. Although multiple languages may be spoken in one place, many areas are dominated by one language. Future work on the patterns of language diversity would benefit from the development of a novel spatial constraint model that generates the pattern of language richness expected if the observed language ranges maintained their sizes but were placed randomly within geographical domains (constrained by a realistic limit on the maximum number of overlapping language ranges). Such an approach would provide a more realistic null model in which the fact is recognized that, in the absence of other gradients (e.g., environmental, biological, social), language richness is likely not to be spatially uniform, as has been assumed in current analytical approaches.

Perhaps the greatest challenge for future research is that previous studies have been, almost without exception, based on regression and correlation. Because correlation does not guarantee direct causation, the mechanisms underlying the correlates of diversity remain poorly understood (Gotelli et al. 2009). Simulation modeling has recently been advanced in biogeography to provide explicit tests of species diversification mechanisms (Rangel et al. 2007, Colwell and Rangel 2010; see Gotelli and colleagues [2009] for a review of the approach). These models have the potential to simulate different scenarios for the origin, spread, and extinction of languages in an environmentally heterogeneous landscape on the basis of the constraints defined by proposed mechanisms of language diversification. This modeling approach empowers the direct testing of specific diversification mechanisms, can incorporate variation in these mechanisms, can account for nonlinear and indirect causal pathways, and can include any geometric constraints specified by null models (Gotelli et al. 2009). The simulation models work as a series of quasiexperiments, allowing the modeler to hold certain factors constant to isolate the impact of particular processes on emergent patterns of language distribution (Rangel et al. 2007). In addition, these simulation models can be predictive, producing maps with language ranges and simulated language phylogenies. In turn, the simulated language range sizes, language diversity patterns, and language phylogenies can be compared with available empirical patterns in order to provide a more statistically robust means

of inferring the role that specific variables and underlying diversification mechanisms play in determining language diversity patterns (Rangel et al. 2007). Simulation modeling is most effective when it carefully isolates the factors of interest and avoids unnecessary complexity that can make the model's results difficult to interpret. The main challenge that the simulation approach presents is the need to define and parameterize the specific processes hypothesized to be the determiners of language diversity patterns (Gotelli et al. 2009).

Theoretical considerations for future studies: The mechanisms behind diversification

In the empirical studies reviewed above, associations have been proposed between linguistic diversity and a variety of social and ecological factors. However, there remain gaps in our knowledge about the specific mechanisms that drive linguistic diversification, an important area if we are to build a mechanistic understanding of the process. Although in some previous studies (e.g., Birdsell 1953, Nettle 1998, Currie and Mace 2009) potential mechanisms have been suggested, they have rarely been explicitly tested. Moreover, there is no comprehensive review of the mechanisms underlying linguistic diversification. In the next section, we address this by discussing a series of potential mechanisms that are involved in language cladogenesis and in the formation of linguistic disparity.

Mechanisms driving language cladogenesis. We propose that four key processes (neutral change, movement, contact, and selection) drive many of the patterns in language richness discussed above. Parallels between linguistic change and biological evolution have been noted since Darwin (1859). For example, both domains involve the transmission of discrete heritable units: These are genes in biology and include units such as words and morphosyntax in linguistics. However, the process of inheritance differs between the two domains: Genes are inherited from parents, whereas language is acquired not only from parents but also from peer groups and the general community. The heritable units in both language and biology can change (i.e., undergo mutation), and mutation occurs at variable rates. In linguistics, it has been established that some types of words are quite resistant to change, whereas others, including slang and words for technological concepts, may evolve rapidly (e.g., Tadmor 2009). Just as in biological evolution, neutral change in heritable language units can accumulate in speech communities. If these communities are isolated for a sufficient time, these neutral changes may eventually disrupt mutual comprehension with other communities. As with biological speciation, isolation, population size, and founder effects may all interact with neutral changes in languages to drive linguistic diversification.

Because languages are markers of human groups, language diversification is also a byproduct of group boundary formation (Foley 2004). These boundaries can be physical

(e.g., mountains) or social (e.g., castes, clans). In addition, groups can exist at multiple levels, such that any individual may belong to multiple nested groups (and multiple non-nested groups in the case of multilingual individuals). For example, unless you are reading this article in translation, you speak English, and there is a clear boundary delineating English speakers and those who do not speak English. However, among English speakers, there are also many recognizable subgroups based on regional dialects, age groups, and class differences, among other variables. To understand the drivers of geographical patterns of linguistic diversity, we must understand the relative influence of different factors that either construct or break down the boundaries between human groups. In this review, we have highlighted the lack of understanding of the mechanisms by which the environmental and social factors associated with linguistic diversity may affect group boundary formation and, ultimately, linguistic diversification. We argue that group boundaries are shaped by the independent and combined forces of movement of groups of people, contact among groups of people, and selection.

Although many underlying factors may influence the movement of groups of people (e.g., population growth, war, famine, exploration, trade), movement processes themselves can lead to group isolation, which is a crucial outcome for language diversification. Multiple historical cases document new languages that developed after groups migrated to colonize remote lands, where they had limited contact with outside groups. For example, the movement of Polynesian people from the Marquesas to the Hawaiian Islands approximately 1000 years ago led to relative isolation of the Hawaiian population and the development of the Hawaiian language.

In contrast, when a group moves into an already populated area, contact with other groups becomes important in shaping linguistic diversity. Theoretically, groups that come into contact may remain intact, with their languages undergoing little or no change. In other cases, contact can result in an expanding population replacing or displacing an existing population and its language (Bellwood 2009). Contact can also result in the expansion of the geographical range of a language without the replacement or displacement of existing populations through cultural assimilation, cultural diffusion, and language adoption (Bellwood 2009). More commonly, contact may contribute to patterns of linguistic disparity by influencing language change through borrowing. Borrowing can affect many different aspects of a language, including the lexicon (i.e., vocabulary), syntax (i.e., sentence-level grammar), and phonology (i.e., sound systems). Contact may also lead to the formation of new languages, such as creoles and mixed languages (Thomason and Kaufman 1989). Linguists have considered the extent to which structural features of languages may play a role in facilitating or retarding language contact and transfer. Although structural compatibility facilitates the transfer of features from one language to another (Sapir 1921), it is

also clear that language contact may take place even among disparate languages (Thomason and Kaufman 1989). The two linguistic factors that most affect the degree of contact seem to be the degree of familiarity that speakers have with each other's languages and how tightly integrated a particular linguistic feature is in the linguistic system, with closely integrated units (such as morphemes, the smallest semantic unit of a language) being more difficult to borrow than loosely integrated items, such as words (Thomason and Kaufman 1989).

Linguistic selection occurs when a particular way of speaking is favored under particular conditions. Because not every individual possesses the same characteristics and because conditions vary, selection pressures can lead to linguistic diversification. Selection can arise from both social and environmental conditions. Social status, or the variability in prestige held by different groups in a society, can have a strong relationship with language use. In turn, languages may vary systematically with gender, social class, age group, education level, and religion (Labov 2010). In addition, social and technological factors also play a major role in shaping livelihood strategies, access to and distribution of resources, and the ability to mobilize human and material resources in response to threats (and also demography; see below).

A second sense of the term *selection* entails choices that individuals make with respect to which language or languages they speak. If a particular language is associated with social or economic advantage, ethnolinguistic groups will tend to favor that language, and the language will tend to prosper either from demic change or from cultural diffusion from one group to another as a result of prestige effects (Foley 2004). The clearest example of such a process comes from modern instances of language endangerment in countries such as the United States and Australia, where the languages of disadvantaged indigenous and migrant groups have low levels of intergenerational transfer and shifts to locally dominant languages are common (Grenoble and Whaley 1998). Differences in competitive advantage across an ethnolinguistic group's range can also spur technological innovations as marginal sectors of the population seek improved livelihood strategies, which can ultimately lead to group boundary formation and linguistic diversification. Such shifts may occur through individuals making economic choices; they also occur as a result of political coercion, oppression, or segregation (Currie and Mace 2009).

The outcomes of the four main processes of linguistic diversification (neutral change, movement, contact, and selection) and their interactions are, in turn, influenced by three key variables: demography, environmental heterogeneity, and time (e.g., Birdsell 1953). Increases in population size can drive the movements of people as resources become scarce, and these movements can lead to linguistic diversification. In addition, relative population densities are key in determining the outcome of encounters among

language groups, with higher densities often conferring a competitive advantage. High population densities are often a result of technological and political factors. For example, technological advances, such as farming, have also permitted higher population densities, which have led to increased political complexity. Politically complex societies living at higher densities tend to have increased levels of labor specialization. This provides a feedback mechanism, further driving technological advances and increasing the competitive advantage of one group over others. The expansion of relatively politically complex farming groups has radically changed the landscape of language diversity across much of the planet over the last 10,000 years as the languages of the farming groups displaced or assimilated the languages of many hunter-gatherers (Currie and Mace 2009). Relative demographics are also a key factor determining the outcome of contact events. Expanding groups that maintain higher densities and have a competitive advantage tend to replace or displace existing groups that are at lower densities and lack a competitive advantage (Foley 2004). However, even though agriculture is recognized as a driving force of Holocene linguistic expansion, there is evidence for extensive spread in hunter-gatherer families during a similar period (e.g., Algonquian; Haas 1966).

Just as environmental heterogeneity affects biological processes, it may also shape the outcomes of linguistic diversification. Large expanses of water or high levels of topographic complexity can impede movement and increase the potential for isolation (Gavin and Sibanda 2012). Following the movement of a group into such isolated landscapes, drift has a greater chance of driving diversification. Environmental heterogeneity can also interact with selection to produce specialization, because different livelihood strategies are better suited to different conditions. This specialization can lead to group boundary formation and, therefore, to linguistic diversification (e.g., the difference between pastoralists and agriculturalists).

Finally, time is a vital precondition of the linguistic diversification processes. Movement, contact, and selection all shape group boundaries, but these boundaries must be in place for a sufficient time in order for linguistic diversification to occur. And over time, social and environmental conditions are in flux, altering the probability of additional movement, contact, and selection pressures. It must be emphasized that although we focus here on demography, society, complexity, and environment as broad determinants of linguistic change, we do not deny the role of individuals as agents of change.

Future considerations for examining language disparity. Although it is uncontroversial that rates of linguistic change vary (Thomason and Kaufman 1989, Nettle 1999c, Campbell and Poser 2008), there is no consensus regarding which factors most influence rates of change. Sociolinguistic factors are major generators of variation in languages: Speakers consciously—or more often, unconsciously—amplify minor

variations in linguistic performance (Milroy 1992, Labov 1994, 2001, Trudgill 2005). These minor variations also act as reservoirs of diversity, because of a general tendency to use any localized variation as a social signal. An important insight from sociolinguistics is that language functions as a mechanism for marking social boundaries both within and between communities (Labov 1963, Thurston 1987, Dorian 1994). The causal factors of linguistic disparity are often addressed under the heading of *linguistic complexity*. It may be that complexity accrues more or less randomly but stays around only in those special sociolinguistic contexts in which it is not selected against. Trudgill (2011) listed five major complexity-producing social factors: small group size, dense social networks, large amounts of shared information, high stability, and low levels of contact (see also Labov 2010). Nettle (1999c) argued that rates of change are greater in small populations, because the smaller the number of speakers of a language is, the less time is required for changes to diffuse across the entire speech community. Conversely, Milroy (1992) and sociolinguists such as Trudgill (2005) have argued that smaller communities exhibit slower rates of change, because the dense and multiplex social network structures that such groups exhibit are known to be resistant to the introduction of innovations (Granovetter 1983). Therefore, the relationship between population size and rates of change is not at all straightforward.

Language contact has also been suggested as a cause of increased rates of change, primarily on the basis of the observation that languages in contact not only show the results of contact-induced change but also tend to show other language-internal changes, as well (Trudgill 2011). More specifically, languages undergoing severe population reduction can show extensive changes over just a few generations (e.g., Nyulnyul; McGregor 2002). In addition, a language that is frequently acquired by adult learners tends to lack the complexity of languages that are learned only by children, because adult acquisition acts as a selective pressure against complexity (Trudgill 2005, 2011). Lupyán and Dale (2010) hypothesize that greater complexity increases redundancy and facilitates learning by infants, but others point out that infant language learning proceeds by different means than adult language learning and is not subject to such constraints (Krashen 1982).

Finally, group cultural factors and human agency affect both the rates and the types of change that languages undergo. One famous case involves the languages of the Vaupés region of Amazonia (Epps 2006), where the combination of widespread exogamy and strong cultural prohibitions against language mixing have led to languages showing almost no lexical borrowings but strong structural convergence. Another positive pressure for increasing disparity is the phenomenon known as *esoterogeny*, the sociolinguistic drive for communities to differentiate themselves from outsiders (Thurston 1987). In one of the few studies to empirically test any of the theories related to linguistic disparity, the conclusion was that languages spoken

by large groups with adult learners tend to be morphologically less complex (Lupyán and Dale 2010).

Researchers have also noted that the many pidgin and creole languages of the world share a considerable level of common structure. Although some scholars consider this an accident of history, others argue that the low levels of disparity within creole grammars reflect universal principles of human language (first proposed by Bickerton [1981]; also see Seuren and Wekker [1986]). However, no quantitative studies have been carried out to test these hypotheses (but see the Atlas of Pidgin and Creole Language Structures project; Michaelis et al. 2013). There have also been suggestions that the historical processes acting on hunter-gatherer languages are qualitatively different from the processes acting on languages of sedentary communities, but subsistence type has not been shown to add any explanatory power to the sociolinguistic determinants of disparity discussed above (Bowerman 2010). In addition, a wide range of language-internal factors influence the emergence of linguistic disparity, such as the influence of cognition on the architecture of language (see Dunn and colleagues [2011] and Labov [1994] for additional information).

Conclusions

Understanding the key factors shaping geographic patterns in language diversity is a crucial task, given the value of language diversity. For example, studies of language diversity can help build our understanding of human history, cultural evolution, and the complexity of human cognition (e.g., Currie et al. 2010). Unfortunately, language diversity is rapidly decreasing, with an estimated 50% of the extant languages to be extinct before the end of the next century (Krauss 1992). Understanding the attributes of modern human society that drive language extinction and how these processes shape the geographical patterns of language diversity are areas in urgent need of research attention. As is the case with biodiversity, knowledge of the factors that lead to diversification and extinction will likely be crucial in planning effective language conservation strategies.

In the present article, we have both reviewed previous studies and made a theoretical contribution to the study of human linguistic diversity. What is needed now is sustained and detailed research attention to these patterns that takes into account the theoretical complexities and methodological considerations that we have outlined in the second section of the article. We believe that the next frontier for this field is to begin to test (in part using techniques drawn from ecology and evolutionary biology) each of these hypothesized linguistic diversification mechanisms in order to determine the degree to which these processes shape different linguistic diversity patterns (language richness, phylogenetic language diversity, and language disparity). In this way, future analyses will further our understanding of the individual threads that form the fabric of human history and may be able to answer fundamental questions of cultural and linguistic evolution.

Acknowledgments

This work was supported by the National Evolutionary Synthesis Center, in Durham, North Carolina.

References cited

- Atkinson QD, Meade A, Venditti C, Greenhill SJ, Pagel M. 2008. Languages evolve in punctuational bursts. *Science* 319: 588.
- Beale CM, Lennon JJ, Yearsley JM, Brewer MJ, Elston DA. 2010. Regression analysis of spatial data. *Ecology Letters* 13: 246–264.
- Bellwood P. 2009. The dispersals of established food-producing populations. *Current Anthropology* 5: 621–626.
- Bickerton D. 1981. *The Roots of Language*. Karoma.
- Birdsell JB. 1953. Some environmental and cultural factors influencing the structuring of Australian aboriginal populations. *American Naturalist* 87: 171–207.
- Bowern C. 2010. Correlates of language change in hunter–gatherer and other “small” languages. *Language and Linguistics Compass* 4: 665–679.
- Burnham KP, Anderson DR. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer.
- Campbell L, Poser WJ. 2008. *Language Classification: History and Method*. Cambridge University Press.
- Cashdan E. 2001. Ethnic diversity and its environmental determinants: Effects of climate, pathogens, and habitat diversity. *American Anthropologist* 103: 968–991.
- Colwell RK, Rangel TF. 2010. A stochastic, evolutionary model for range shifts and richness on tropical elevational gradients under Quaternary glacial cycles. *Philosophical Transactions of the Royal Society B* 365: 3695–3707.
- Colwell RK, Rahbek C, Gotelli N. 2004. The mid-domain effect and species richness patterns: What have we learned so far? *American Naturalist* 163: E1–E23.
- Currie TE, Mace R. 2009. Political complexity predicts the spread of ethnolinguistic groups. *Proceedings of the National Academy of Sciences* 106: 7339–7344.
- . 2012. The evolution of ethnolinguistic diversity. *Advances in Complex Systems* 15 (art. 1150006). doi:10.1142/S0219525911003372
- Currie TE, Greenhill SJ, Gray RD, Hasegawa T, Mace R. 2010. Rise and fall of political complexity in island South-East Asia and the Pacific. *Nature* 467: 801–804.
- Darwin C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray.
- Dorian NC. 1994. Choices and values in language shift and its study. *International Journal of the Sociology of Language* 110: 113–124.
- Dunn M, Greenhill SJ, Levinson SC, Gray RD. 2011. Evolved structure of language shows lineage-specific trends in word-order universals. *Nature* 473: 79–82.
- Epps P. 2006. The Vaupés Melting Pot: Tucanoan Influence on Hup. Pages 267–289 in Aikhenvald A, Dixon R, eds. *Grammars in Contact: A Cross-Linguistic Typology*. Oxford University Press.
- Faith DP. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61: 1–10.
- Fincher CL, Thornhill R. 2008. A parasite-driven wedge: Infectious diseases may explain language and other biodiversity. *Oikos* 117: 1289–1297.
- Foley RA. 2004. The evolutionary ecology of linguistic diversity in human populations. Pages 61–71 in Jones M, ed. *Traces of Ancestry: Studies in Honour of Colin Renfrew*. McDonald Institute for Archaeological Research.
- Fotheringham AS, Brunson C, Charlton M. 2002. *Geographically Weighted Regression: The Analysis of Spatially Varying Relationships*. Wiley-Blackwell.
- Freckleton RP. 2009. The seven deadly sins of comparative analysis. *Journal of Evolutionary Biology* 22: 1367–1375.
- Gavin MC, Sibanda N. 2012. The island biogeography of languages. *Global Ecology and Biogeography* 21: 958–967.
- Gorenflo LJ, Romaine S, Mittermeier RA, Walker-Painemilla K. 2012. Co-occurrence of linguistic and biological diversity in biodiversity hotspots and high biodiversity wilderness areas. *Proceedings of the National Academy of Sciences* 109: 8032–8037.
- Gotelli NJ, et al. 2009. Patterns and causes of species richness: A general simulation model for macroecology. *Ecology Letters* 12: 873–886.
- Granovetter M. 1983. The strength of weak ties: A network theory revisited. *Sociological Theory* 1: 201–203.
- Gray RD, Drummond AJ, Greenhill SJ. 2009. Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science* 323: 479–483.
- Grenoble LA, Whaley LJ. 1998. *Endangered Languages: Language Loss and Community Response*. Cambridge University Press.
- Haas MR. 1966. Wiyot-Yurok-Algonkian and problems of comparative Algonkian. *International Journal of American Linguistics* 32: 101–107.
- Hamilton MJ, Milne BT, Walker RS, Burger O, Brown JH. 2007. The complex structure of hunter-gatherer social networks. *Proceedings of the Royal Society B* 274: 2195–2202.
- Harrison DK. 2007. *When Languages Die: The Extinction of the World’s Languages and the Erosion of Human Knowledge*. Oxford University Press.
- Johnson AW, Earle T. 2000. *The Evolution of Human Societies: From Foraging Groups to Agrarian State*, 2nd ed. Stanford University Press.
- Kerr JT, Packer L. 1997. Habitat heterogeneity as a determinant of mammal species richness. *Nature* 385: 252–254.
- Krashen SD, ed. 1982. *Child–Adult Differences in Second Language Acquisition*. Newbury House.
- Krauss M. 1992. The world’s languages in crisis. *Language* 68: 4–10.
- Labov W. 1963. The social motivation of a sound change. *Word* 19: 273–309.
- . 1994. *Principles of Linguistic Change*, vol. 1: Internal Factors. Wiley-Blackwell.
- . 2001. *Principles of Linguistic Change*, vol. 2: Social Factors. Wiley-Blackwell.
- . 2010. *Principles of Linguistic Change*, vol. 3: Cognitive and Cultural Factors. Wiley-Blackwell.
- Laitin DD, Moortgat J, Robinson AL. 2012. Geographic axes and the persistence of cultural diversity. *Proceedings of the National Academy of Sciences* 109: 10263–10268.
- Loh J, Harmon D. 2005. A global index of biocultural diversity. *Ecological Indicators* 5: 231–241.
- Lupyan G, Dale R. 2010. Language structure is partly determined by social structure. *PLOS ONE* 5 (art. e8559).
- Mace R, Pagel M. 1995. A latitudinal gradient in the density of human languages in North America. *Proceedings of the Royal Society B* 261: 117–121.
- Manne LL. 2003. Nothing has yet lasted forever: Current and threatened levels of biological and cultural diversity. *Evolutionary Ecology Research* 5: 517–527.
- McGregor W. 2002. Structural changes in language obsolescence: A Kimberley (Australia) perspective. *SKY Journal of Linguistics* 15: 145–185.
- Michaelis SM, Maurer P, Haspelmath M, Huber M. 2013. The Atlas of Pidgin and Creole Language Structures (APiCS). APiCS. (2 April 2013; [http://lingweb.eva.mpg.de/apics/index.php/The_Atlas_of_Pidgin_and_Creole_Language_Structures_\(APiCS\)](http://lingweb.eva.mpg.de/apics/index.php/The_Atlas_of_Pidgin_and_Creole_Language_Structures_(APiCS)))
- Michalopolous S. 2008. *The Origins of Ethnolinguistic Diversity: Theory and Evidence*. Tufts University. Discussion Paper Series no. 725.
- Milroy J. 1992. Social network and prestige arguments in sociolinguistics. Pages 146–162 in Bolton K, Kwok H, eds. *Sociolinguistics Today: International Perspectives*. Routledge.
- Moore JL, Manne L, Brooks T, Burgess ND, Davies R, Rahbek C, Williams P, Balmford A. 2002. The distribution of cultural and biological diversity in Africa. *Proceedings of the Royal Society B* 269: 1645–1653.

- Naroll R. 1965. Galton's problem: The logic of cross-cultural research. *Social Research* 32: 428–451.
- Nettle D. 1996. Language diversity in West Africa: An ecological approach. *Journal of Anthropological Archaeology* 15: 403–438.
- . 1998. Explaining global patterns of language diversity. *Journal of Anthropological Archaeology* 17: 354–374.
- . 1999a. *Linguistic Diversity*. Oxford University Press.
- . 1999b. Linguistic diversity of the Americas can be reconciled with a recent colonization. *Proceedings of the National Academy of Sciences* 96: 3325–3329.
- . 1999c. Is the rate of linguistic change constant? *Lingua* 108: 119–136.
- . 2009. Ecological influences on human behavioural diversity: A review of recent findings. *Trends in Ecology and Evolution* 24: 618–624.
- Pagel M, Atkinson QD, Meade A. 2007. Frequency of word-use predicts rates of lexical evolution throughout Indo-European history. *Nature* 449: 717–720.
- Rangel TF, Diniz-Filho JA, Colwell RK. 2007. Species richness and evolutionary niche dynamics: A spatial pattern-oriented simulation experiment. *American Naturalist* 170: 602–616.
- Renfrew C. 1994. World linguistic diversity. *Scientific American* 270: 116–123.
- Sapir E. 1921. *Language: An Introduction to the Study of Speech*. Harcourt, Brace.
- Seuren PAM, Wekker HC. 1986. Semantic transparency as a factor in creole genesis. Pages 57–70 in Muysken P, Smith N, eds. *Substrata Versus Universals in Creole Genesis*. John Benjamins.
- Smith EA. 2001. On the coevolution of cultural, linguistic, and biological diversity. Pages 95–117 in Maffi L, ed. *On Biocultural Diversity: Linking Language, Knowledge, and the Environment*. Smithsonian Institution Press.
- Stepp JR, Cervone S, Castaneda H, Lasseter A, Stocks G, Gichon Y. 2004. Development of a GIS for global biocultural diversity. *Policy Matters* 13: 267–270.
- Stepp JR, Castaneda H, Cervone S. 2005. Mountains and biocultural diversity. *Mountain Research and Development* 25: 223–227.
- Sutherland WJ. 2003. Parallel extinction risk and global distribution of languages and species. *Nature* 423: 276–279.
- Tadmor U. 2009. Loanwords in the world's languages: Findings and results. Pages 55–75 in Haspelmath M, Tadmor U, eds. *Loanwords in the World's Languages: A Comparative Handbook*. De Gruyter Mouton.
- Thomason SG, Kaufman T. 1989. *Language Contact, Creolization, and Genetic Linguistics*. University of California.
- Thurston WR. 1987. *Processes of Change in the Languages of North-Western New Britain*. Australian National University.
- Tomarken AJ, Waller NG. 2005. Structural equation modeling: Strengths, limitations, and misconceptions. *Annual Review of Clinical Psychology* 1: 31–65.
- Trudgill P. 2005. On the complexity of simplification. *Linguistic Typology* 8: 384–388.
- . 2011. *Sociolinguistic Typology: Social Determinants of Linguistic Complexity*. Oxford University Press.
- Willig M, Kaufman D, Stevens R. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34: 273–309.

Michael C. Gavin (michael.gavin@colostate.edu) and Joe McCarter are affiliated with the Department of Human Dimensions of Natural Resources at Colorado State University, in Fort Collins; MCG is also affiliated with the School of Geography, Environment, and Earth Sciences at Victoria University of Wellington, in Wellington, New Zealand. Carlos A. Botero is affiliated with the Initiative for Biological Complexity and with the Southeast Climate Science Center, and Robert R. Dunn is affiliated with the Department of Biology, at North Carolina State University, in Raleigh. Claire Bownen is affiliated with the Department of Linguistics at Yale University, in New Haven, Connecticut. Robert K. Colwell is affiliated with the Department of Ecology and Evolutionary Biology at the University of Connecticut, in Storrs, and with the University of Colorado Museum of Natural History, in Boulder. Michael Dunn is affiliated with the Evolutionary Processes in Language and Culture Group, at the Max Planck Institute for Psycholinguistics, in Nijmegen, the Netherlands. Russell D. Gray is affiliated with the Department of Psychology at the University of Auckland, New Zealand. Kathryn R. Kirby is affiliated with the Department of Ecology and Evolutionary Biology and with the Department of Geography and Planning at the University of Toronto, Canada. Adam Powell is affiliated with the University College London Genetics Institute, in the United Kingdom. Thiago F. Rangel is affiliated with the Department of Ecology at the Federal University of Goiás, in Goiás, Brazil. John R. Stepp is affiliated with the Department of Anthropology at the University of Florida, in Gainesville. Michelle Trautwein is affiliated with the Nature Resource Center, at the North Carolina Museum of Natural Sciences, in Raleigh. Jennifer L. Verdolin is affiliated with the National Evolutionary Synthesis Center, in Durham, North Carolina. Gregor Yanega is affiliated with the Department of Biology at Pacific University, in Forest Grove, Oregon.