



What you can do for evolutionary developmental linguistics

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Abstract

A growing number of linguistic attempts to explain how languages change use cultural-evolutionary models involving selection or drift. Developmental constraints and biases, which take center stage in evolutionary developmental biology or evo-devo, seem to be absent within this framework, even though linguistics is home to numerous notions of constraint. In this paper, we show how these evo-devo concepts could be applied to linguistic change and why they should. This requires some conceptual groundwork, due to important differences between linguistic and biotic evolution. In biological evolution, *development* generates the *organism's* variable traits on which selection and drift act. In linguistic evolution by analogy, we say development generates the *linguistic* variants on which selection and drift can act. “Linguistic development” then picks out how individual speakers produce and comprehend language. It involves much more than just learning. Using this broad notion of development, we distinguish between different types of *bias* that could operate in the processes of linguistic innovation and transmission, which correspond to genetic mutation and biological reproduction, respectively. Having thus sharpened our conceptual toolbox, we then reanalyze two well-documented cases of linguistic change and show that, in both these cases, linguists have only considered Neo-Darwinian evolutionary explanations, falsely deploying an exclusive disjunction of selection and drift. We show that there is at least a third relevant alternative in these examples, namely developmental constraint or bias in the sense we explicate here.

Keywords Philosophy of linguistics · Linguistic evolution · Cultural evolution · Neo-Darwinism · Evolutionary developmental biology (evo-devo) · Developmental constraint · Developmental bias

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1 Introduction

While linguists acknowledge the similarity of linguistic and biological change with respect to patterns of diversification, they are divided when it comes to evolutionary mechanisms as drivers of language change (Gontier, 2018). Thus, while basically the same concepts and inference methods are used to reconstruct the phylogenies of languages and of biological taxa, linguistics lacks some of the causal mechanisms and factors that biology uses to explain phyletic change. In particular, cultural-evolutionary approaches to linguistic change have been focused on selection and drift as the main mechanisms of change, ignoring developmental bias and constraints. In this paper, we argue that these are unconsidered alternative explanations of linguistic change and that linguists should reckon with these evolutionary factors just like evolutionary biologists do.

Since the 1980s, evolutionary biology has taken a turn from a predominantly Neo-Darwinian approach focusing on adaptation, selection and drift to using a more diverse set of explanatory strategies including in particular those developed as part of evolutionary developmental biology or ‘evo-devo’ (Gilbert et al., 1996; Love, 2024; Müller, 2007; Raff, 2000). Is there also such a developmentalist turn observable in evolutionary linguistics? To answer this question, it should first be noted that since the mid-20th Century, much of linguistics has been dominated by the theory and associated research program of generative grammar, which abstracts completely from any biological facts as well as from individual variation (Chomsky, 2015). While Chomsky himself has shown a sustained interest in integrating the generative grammar approach with evo-devo, he and other linguists working with the same theoretical framework mainly see its role as explaining the origin of the language *faculty* (Berwick & Chomsky, 2016; Chomsky, 2010), which is not our concern in this paper. Our focus is exclusively on how languages evolve¹ in populations of speakers who are already endowed with this faculty, i.e., *linguistic* evolution and not *language* evolution (Bickel et al., 2024).

Things look quite different when it comes to explaining how individual languages change, which is as distinct from explaining the origin of the language faculty as explaining the diversification of life is from explaining the origin of life. Linguistic evolution takes place in populations of speakers that share their language faculty. Different explanatory frameworks have been developed for this purpose, some of which do not appeal to any biological concepts at all, while others do, and some explicitly take an evolutionary approach (Christiansen & Kirby, 2003; Croft, 2000; Pagel, 2017; Tallerman & Gibson, 2011). By “evolutionary approach” we mean treating individual languages as inherently variable within populations of speakers and taking variations to be *culturally transmissible* by individuals adopting

¹ It is controversial whether language and cultural change in general are *bona fide* instances of Darwinian evolution or merely analogous to it (Fracchia & Lewontin, 1999; Love & Wimsatt, 2019; Reydon & Scholz, 2015). We take the view that evolutionary concepts as applied to cultural and linguistic change may have started their life as analogies, but that they have since been developed in a way that makes them part of full-blown scientific explanations and hence more than just analogies.

Table 1 Some parallels between biological and linguistic evolution (Pagel 2017)

Biological evolution	Language evolution
Discrete heritable units (e.g., nucleotides, amino acids, and genes)	Discrete heritable units (e.g., words, phonemes, and syntax)
DNA copying	teaching, learning and imitation
Mutation (e.g., many mechanisms yielding genetic alterations)	Innovations (e.g., formant variation, mistakes, sound changes, and introduced sounds and words)
Homology	Cognates
Natural selection	Social selection and trends
Drift	Drift
Speciation	Language or cultural splitting
Concerted evolution	Regular sound change
Horizontal gene transfer	Borrowing
Hybridization (e.g., horse with zebra and wheat with strawberry)	Language Creoles (e.g., Surinamese)
Geographic clines	Dialects and dialect chains
Fossils	Ancient texts
Extinction	Language death

grammatical features, words and word variants as well as word meanings from other speakers (Pagel, 2009). Such evolutionary approaches have also been described as a “return to a pre-Chomskyan conception of language” (Chater & Christiansen, 2011), and they have gained some popularity in recent years, even though they are not universally accepted by the linguistics community. The present work is exclusively about the latter approach; thus, we ask readers to bear in mind that we are making no claims about the relative merits of a broadly Chomskyan² versus a cultural-evolutionary approach to language, nor are we interested here at all in the evolution of the language *faculty*. Thus, when we claim that linguists have largely ignored developmental constraints and biases, as we are going to, we mean these terms in a very specific sense that is tied to the cultural-evolutionary framework. We explicate this sense in Sections 2 and 3.

When we now turn to cultural-evolutionary explanations of linguistic change, we notice that they are typically framed exclusively in Neo-Darwinian terms.³ A striking example is Pagel (2017), who compiles some 13 parallels between biological and linguistic evolution (see Table 1). Developmental constraints and biases are not on his list. We argue that they are unjustifiably absent because developmentalist explanations in the sense we explicate here are relevant alternative explanations to selection and drift. The consideration of relevant alternatives is a norm of scientific

² See Nefdt (2023) for a recent critique of Chomsky’s approach.

³ We mean “Neo-Darwinian” in a sense that includes the concept of exaptation (Gould & Vrba, 1982), which has been applied to linguistic change (Lass, 1990; Van de Velde & Norde, 2016).

inquiry that ensures that appropriate evidentiary standards be used when inferring mechanisms of evolutionary change (Lloyd, 2015). We also show that this requires a new way of conceptualizing linguistic development.⁴ In biological evolution, *development* generates the *organism's* variable traits on which selection and drift act. Therefore, the analogy in linguistic evolution holds that development generates the *linguistic* variants on which selection and drift can act. “Linguistic development” then picks out the sum total of the processes by which individual speakers produce and comprehend language. It does not just pick out biological development and it involves much more than just language acquisition and learning, or so we shall argue.

We structure our argument as follows: We would like to show that the cultural evolutionary framework of linguistic change can be extended to include explanatory strategies known from evo-devo, expanding the usual stock of evolutionary explanatory strategies from two to three. Where usually just functional and neutral explanations are considered within a cultural-evolutionary framework, we propose to add as relevant alternative strategies *developmental* explanations, in a very specific sense to be explicated. This will require some conceptual groundwork, which we provide here. Furthermore, we propose that in such an extended framework, specific cases of language change may be explained by any combination of the three types of causes, which can pull in the same or in different directions (see Novick, 2023 for a similar account in the context of biology). One fruit of this shift in framework will be new questions which require new models to be developed, new observations to be made, and especially new experiments to be undertaken. This will lead to a more accurate picture of the causes of linguistic change over time.

In the following two sections, we present some basic concepts intended for an extended evolutionary framework, adapting concepts from Neo-Darwinism as well as from evo-devo to linguistic change. We attempt to stay as close as possible to the corresponding biological concepts and discuss how they can be fitted to linguistic change. In Section 3, we develop a concept we call *variation bias* and compare it to existing notions. Sections 4 and 5 present re-analyses of two cases of linguistic change, namely word variability and grammatical stasis in English (Section 4) and divergence and convergence in the 138 recorded languages of the Vanuatu archipelago, the “Galapagos of language evolution” (Goddard, 2016), in Section 5. In both cases, we show that variation bias is an unconsidered relevant alternative to selection and drift explanations. We close Section 5 by raising the methodological problem of the kinds of evidence that could distinguish these various factors in practice. Section 6 draws together our conclusions.

⁴ As far as we can ascertain, no one has proposed an evo-devo account of linguistic change in the linguistic literature. However, Cathcart (2024), like us a member of the NCCR Evolving Language, has just published an excellent example of how our framework of distinguishing evolutionary factors can be applied to empirical problems in linguistics focusing on consonant avoidance.

2 Basic concepts for an extended evolutionary-developmental framework

In what follows, we develop an extended framework for linguistic evolution. Then, we will argue that constraints and developmental biases in the specific sense in which we understand them are relevant alternatives to selection and drift within a cultural-evolutionary framework. Table 2 contains what we propose to be linguistic analogs of standard evolutionary as well as evo-devo concepts from biology. This is followed by a more detailed account of these concepts.

Development It would be a mistake to consider only language learning in infants or adults as linguistic development, because it is not the only process that has an impact on linguistic evolution. It may not even be an important factor (Widmer et al., 2021). We propose to construe development broadly as the sum of all processes involved in language acquisition, learning, production, hearing and comprehension over a speaker's lifetime. Hearing and comprehension must be included because the way in which humans speak or sign is in part a result of how they process visual and auditory inputs. In biology, development is the sum of all processes that generate an organism's phenotype. Here, because the phenotype is an individual's verbal and signing behavior, development must include all the processes that are involved in generating and controlling this behavior. Just as biotic evolution changes developmental programs, linguistic evolution changes the processes that generate and control verbal and signing behavior. Just as the developmental processes that form individual organisms constrain their evolution, the processes that generate verbal and

Table 2 Proposed linguistic analogs of evolutionary and evo-devo concepts

<i>Development</i>	The totality of auditory, neuro-cognitive, motor and biomechanical mechanisms involved in language learning, production, hearing and comprehension throughout the life of an individual speaker
<i>Linguistic evolution</i>	The change of human languages over time
<i>Mutation / innovation</i>	The generation of new language variants
<i>Fitness</i>	A propensity of versions of a linguistic form (words, sentence structures, phonemes, etc.) to be copied by speakers who have heard it from other speakers
<i>Selection</i>	The differential reproduction, in a given environment, of specific variants of language types that is due to copying bias, i.e., fitness differences
<i>Copying bias</i>	A propensity of the language producing system to copy some specific variants of language types more frequently than others, which is due to fitness differences
<i>Constraint/developmental bias/variation bias^a</i>	A propensity of the language-producing system to generate some specific variants of language types rather than others which is not due to differential copying
<i>Drift</i>	The differential reproduction of specific variants of language types that is not due to any systematic biases in the generation or transmission of variants

^aIn earlier drafts and conference presentations of this work we used the term “production bias”, but some linguists we spoke to found it confusing because it suggests that such biases arise only in language production, which is not what we intend

signing behavior constrain their culturally transmissible changes and hence their evolution.

The developmental system encompasses the parts of the human that change in the learning of language, so especially the brain but then the physical production systems of respiration at the lungs, phonation in the larynx, and articulation in the mouth (for spoken language, different motor control is relevant to signed language). These systems change through language development and learning and are plastic from the perspective of general human development. The brain structures include much more than the Language Faculty or Module hypothesized to provide the innate capacities for language.

Selection Neo-Darwinian hypotheses that could potentially explain linguistic change in terms of selection have been tested (see Sections 4 and 5). These hypotheses presuppose that there is constant linguistic variation, meaning that speakers produce different variants of a word or expression or also variants in grammatical construction where these variants are generated by stochastic mechanisms, analogous to random mutation in genetics. Some of these variants are transmitted by other speakers more often due to a *copying bias*, resulting in variants outcompeting other variants in the population by a process that is akin to natural selection of heritable traits. The selective environment (Brandon, 1990) responsible for copying biases can be internal to the individual speakers, for example, the ease of processing or memory requirements by the language processing system. Selective pressure on copying of linguistic variants may also be exerted by speech perception mechanisms. Alternatively, it can be related to social factors such as group identity or differentiation pressures.

Fitness According to Darwinian evolutionary theory, selection requires heritable differences in fitness (Lewontin, 1970).⁵ It is controversial to what extent there is a cultural analogue to fitness (Gabora, 2011; Lewens, 2012; Sober, 1992), and such doubts are also applicable to linguistic evolution, which is akin to cultural evolution. The chief difficulty is the way in which cultural variants should be counted. Does each copying event of some replicating unit count towards its fitness? This approach would discount many ways in which culturally transmitted entities can affect behavior without being copied. For this reason, Ramsey and De Block (2017) propose to count as fitness-relevant only the adoption of some culturally transmitted practice by an individual organism (human or not). In the present context, this would mean

⁵ Lewontin's by now canonical account of natural selection presupposes the genotype-phenotype distinction. The reason why this distinction is crucial in biology is that the phenotype has its own degrees of freedom; it is not entirely determined by genotype. Thus, the replicators that are transmitted stably from one generation to the next (e.g., genes) can lead to a range of different phenotypes. This can have consequences for the evolutionary dynamics (Lewontin, 2001). By contrast, linguists hold the genotype-phenotype distinction to be irrelevant for linguistic evolution (Bickel et al., 2024). In our view, this distinction could be drawn in linguistics in principle, but this would not make any difference in linguistic practice. Note that without a genotype-phenotype distinction, heritability is always 100%, thus the response to selection is determined by the copying bias alone.

that the fitness of a linguistic variant should be assessed on the basis of the (relative) number of individual speakers who adopt it, counting also those individuals who exhibit other phenotypes at the same time. However, adoption should be strictly separated from innovation in order to keep the conceptual distinction between copying and variation bias (see below) sharp. Selection is conceptually tied to copying biases as measured by fitness differences.

Drift When the variants are transmitted by other speakers more often *not* due to any copying bias, but due to chance or because they happen to have been exposed to one variant more than others, this population will evolve by a process akin to drift (Real & Griffiths, 2010). Over time, drift can change variant frequencies as markedly as selection can, but this change is not predictable/directional like a random walk of coin flips can produce sequences biased towards heads or tails. History plays an enormous role in directing change and a given variant may be very abundant not because of any selective advantage but because its ancestors were very abundant.

Mutation/ innovation The core of Neo-Darwinian theory is often portrayed by a two-step process involving random variation (mutation) and selection (Mayr, 2001). The two steps are independent in the sense that the selective value of a mutation cannot affect the probability of its arising. This is also the precise sense in which mutation is “random” in Neo-Darwinian theory (Sober, 1984). The linguistic analogue of mutation is *innovation* (also called “actuation”), which occurs at the level of individual speakers. Is innovation random in the sense of Neo-Darwinian theory? Linguists distinguish between teleological and non-teleological innovation mechanisms, where the former are deliberately introduced by speakers to serve some purpose (Ohala, 1993). We suggest that the non-teleological innovation mechanisms can be considered as analogues of random mutation in the Neo-Darwinian sense.⁶ What appears to be widely agreed is that mistakes are a possible source of innovation and that they occur independently of their possible functional or selective value. In fact, most of them seem to occur while the speaker is intending to conform to the correct forms (Croft, 2000, p. 119). In sound change, most mistakes that are causative of language change appear to occur at the level of speech perception and they are non-teleological in the sense that they are not deliberately introduced to improve communication (Ohala, 1993). This would mean that, in many cases, linguistic innovation is random in the Neo-Darwinian sense.

What must be emphasized is that the randomness of mutation in this sense does *not* entail that it is unbiased or *isotropic*, i.e., that it occurs with the same probability in all possible directions of change. In biology, there are important biases in the process by which DNA mutations manifest themselves at the phenotypic level. These biases are due to the fact that many DNA mutations are unviable or silent, while others cause phenotypic changes. What is more, due to the specifics

⁶ We will skip a discussion of possible “Lamarckian” mechanisms here. See Kronfeldner (2007) for such a discussion in the context of cultural evolution.

of the developmental process, some phenotypic changes arise more frequently than others, while some are impossible. Biologists call this *developmental bias* (if not all phenotypic variation is equally likely) or *constraint* (if some variation is impossible) and most of them now accept that such biases play an important role in evolution (Brakefield, 2006). Could there be such biases or constraints in linguistic evolution?⁷ This seems conceptually possible, however, unlike in biology, these biases may not be due to the *manifestation* of mutations but due to their very *generation*. Absent a genotype–phenotype distinction (see fn. 5), *all* mutations are manifested, even if they are not noticed or have no evolutionary consequences. Of course, the processes leading to innovations such as reanalysis or grammaticalization may be hidden (Andersen, 2008). But some innovations may have evolutionary consequences, and these consequences are not necessarily determined only by their selective or adaptive value but possibly also by the *frequency by which they arise*, i.e., variation bias. A precondition for this possibility is that innovation be non-isotropic, i.e., not equally likely in all possible directions of change (see the following section). To our surprise, we found no literature in evolutionary linguistics that explicitly considers this option.

This brings us to the new concepts that we would like to introduce, developmental constraint and variation bias. In the following section, we characterize these concepts and contrast it with both selection and drift.

3 Developmental constraint and variation bias

Biologists distinguish between *constraints on form* and *constraints on adaptation* (Amundson, 1994). The former means that some forms cannot be made at all, while the latter means that the forms that would be optimal in terms of adaptedness cannot arise. Developmental biases are all constraints on form where there is an inherent tendency in an organism to produce certain variants or variant combinations rather than others. Such biases prevent, decrease or increase the generation of some variants in the first place (before or independently of inter-individual transmission) and so would be a form of, or analogous to biological, developmental bias (note that we use a broad conception of development that includes language processing in infant as well as adult speakers and fully competent speakers as well as all kinds of language learners, see Table 2). In biotic evolution, the distribution of phenotypes at any given moment can reflect either the purging of some mutations that did arise and were also viable but were removed from the population by selection for other variants, or they could reflect the fact that some phenotypes simply did not form due to developmental constraints or bias. Failure to take such constraints into account can lead to false claims of adaptation. Variation biases should be distinguished from

⁷ It should be noted that none of the usual constraints on language change postulated by linguists correspond to what biologists mean by a developmental constraint or bias. While some linguists postulate constraints that are biological and act at the level of cultural transmission (see Chater and Christiansen 2011, 632), they do not distinguish between copying and variation bias.

fitness differences because they concern the rate by which variants are produced by innovation, whereas fitness differences express a bias in the propagation of variants by copying.

What kind of variation biases could play a role in linguistic evolution? In principle, some of the mechanisms that have been proposed for copying bias such as phonological analogy or cognitive and social factors (Culbertson et al., 2013; Macdonald, 2013; Song & White, 2022) may also lead to variation biases. They would then play a different role; affecting not the rate of copying of variants that the speaker heard from others but the rate by which they generate variants *de novo*. This variability may be non-isotropic, i.e., biased towards some variants; we call this variation bias and claim that it is analogous to developmental bias in evo-devo. Biologists understand that only when variation is isotropic is selection the only explanatory factor relevant for the directionality of change. If variation is non-isotropic, the frequency by which some variants arise must also be taken into account (Novick, 2023). This is why we call variation bias a *relevant alternative* to selection and drift, meaning that it is an alternative possible cause of linguistic change.

A potential example for developmental variation bias is the use of the dental fricative phonemes as in the English "this" and "through" (see Section 4). These phonemes are notoriously difficult for non-native English speakers to acquire, yet of course some do learn to pronounce them. When considering the phonetic morphospace of a given language (a subset of the total human morphospace) there are physical and cognitive constraints involved. The phonetics of a given language are in general hard for non-native speakers to ever master. Some of this is due to the different ways of holding our mouths used in different languages, French being much more forward in the mouth than English. English speakers are simply not used to holding their mouths in that configuration, even though they could learn to do it like learning to play guitar with practice. Other features seem more cognitive. For example, there is evidence that our processing system favors recursively embedded phrases (Widmer et al., 2017). Social factors such as the desire to belong to an ingroup can also provide developmental constraints. We discuss possible variation biases stemming from the presence of multilingual and adult language learners in Sections 4 and 5.

What we would like to submit is that linguistics should consider as relevant alternatives three instead of just two types of evolutionary explanations, namely selection, drift and developmental bias.⁸ Drift should be understood as a propensity of the language-producing system to produce some language variants rather than others that is not due to differential copying. By contrast, selection means that speakers have heard different versions of a language type, e.g., "snuck" versus "sneaked", but they systematically reproduce one of them more frequently. For example, the speaker might favor "snuck" because they want to belong to a cool group that uses this version. So this group would be the selective environment then. Developmental bias occurs when one version is produced more often independently of what the speaker heard. For example, they may have a higher propensity to say "sneaked"

⁸ The process of migration is also included in the Neo-Darwinian framework but nothing we say depends on singling it out.

rather than “snuck” without ever having heard (or remember having heard) an utterance of this word. Whenever there is a propensity to prefer one language type over another that has nothing to do with copying (i.e., transmission between individual speakers) we propose to classify it as developmental bias rather than selection.⁹

The analogy to biological evolution is that differential copying of words or word order is in significant ways like the differential reproduction of heritable traits due to conferral of differential fitness, except that a word doesn’t reproduce by first contributing to the generation of a whole new speaker. Differential generation of words that is not due to copying bias is analogous to developmental bias in biological systems where some phenotypic variants are favored or disfavored not because they are copied more or less often (via biological reproduction) after arising in the population but because they arise more or less often in the first place. Thus, admitting developmental bias allows more fine-grained distinctions with respect to the causes of linguistic change. These causes can fully be integrated, because both variation and copying bias can contribute to changes in the frequency of language types in the population. In the following two sections, we shall reanalyze some case studies from linguistic research to substantiate this thesis.

4 Word variability and stasis

This section and the following one reanalyze two well-known linguistic examples discussed in an explicitly evolutionary framework. Both moreover have, in our view, been shoehorned into a selection vs. drift discussion that is too small to contain them. Each case is improved when discussed in terms of developmental bias as new distinctions can be drawn, new hypotheses can be proposed, and new experiments and observations can be made.

The first case concerns word variability. Words with high (token) frequency empirically exhibit less variability and less change over time than rare words. For example, “to be” is highly irregular in English, German, and the romance languages and also the most frequent verb. One instance of this is that instances of strong verbs in English are more likely than weak verbs to be frequent in the lexicon. Strong verbs are those like “sing”: I sing, I sang, I have sung. Weak verbs are those like “walk”: I walk, I walked, I have walked.

Newberry, Ahern, and colleagues explicitly use a framework from evolutionary biology to investigate how and why common words are less variable (Newberry et al., 2017). We are especially interested in reanalyzing this study because it aims to provide a general approach to studying the evolution, changing relative frequencies, of linguistic units. For their data, they analyzed past tense verb conjugation in the Corpus of American English, with texts between 1810 and 2009. This corpus lets them track the relative abundance of verb form variants like “sneaked” (weak form)

⁹ This distinction may be related to “source-oriented” or “mutational” versus “result-oriented” or “selectional” approaches (Schmidtke-Bode et al., 2018), however, these approaches are usually not presented within a cultural-evolutionary framework.

vs. “snuck” (strong form) diachronically and to track the relative commonness of a given verb relative to other verbs. Doing this, they arrived at much more specific empirical claims than the broad-brush statement: irregular verbs are more common than regular verbs. They know, for example, that “sneaked” dominated until around 1950, when “snuck” started growing in popularity and that today they are almost at parity.

From these empirical trajectories they infer the evolutionary forces responsible for shaping them. Newberry, Ahern, and colleagues claim that after noticing such empirical patterns of word variability, linguists “uniformly invoke selective mechanisms” (Newberry et al., 2017, p. 223). In our framework, these authors are claiming that so far only the selection explanatory strategy has been used. So Newberry, Ahern, and colleagues propose the drift explanatory strategy, which first hypothesizes that observed frequency distributions are the result of neutral drift (neutral meaning that the variants are all treated as functionally equivalent in terms of reproduction success). In this way the explanatory strategies have remained Neo-Darwinian.

The very methodology that they borrow along with drift from evolution carries along with it a Neo-Darwinian bias. The reasoning that Newberry and colleagues follow can be called *null modelling* and it goes as follows (Bausman, 2018; Bausman & Halina, 2018). A selection hypothesis is tested against a drift hypothesis. The drift hypothesis plays the role of the “null model”. Scientists assess the fit of the null model with the empirical data. If the model-fit is poor enough, the null model can be rejected and this warrants accepting the selection explanation of the data. And if the model-fit is good enough, the null model cannot be rejected and this warrants accepting the drift explanation. There are deep worries about the validity of this methodology, but from the perspective of our present critique, the chief difficulty is its implicit denial of any possibility of variation biases when it moves directly to assessing the fit of the drift hypothesis. Some of the change or stasis in the changing frequencies of verb variants could be due to variation bias and constraint.

But the case can easily accommodate considering the roles of variation bias. For example, if phonological analogy operates cognitively by biasing the generation of “dove” over “dived” because, for example “dove” rhymes with “drove”, which is strongly favored over “drived”, this would be a developmental constraint explanation. It is a *cognitive* bias because overregularization is thought to result from the failure of a speaker to retrieve the correct verb form and instead follow the past tense regularization rule (Marcus et al., 1992).¹⁰ Of course, selection (copying bias) could also be responsible for the observed distribution. Our point is that both types of explanation, developmental and selectionist, should be *considered*. This raises an important point about distinguishing selection from developmental constraints.

For Newberry and colleagues, phonological analogies of this kind are a form of selection. In fact, their view is stronger:

¹⁰ Though this explanation is controversial, other proposed mechanisms are also cognitive.

"Forces that bias a speaker towards adopting one form instead of another have been documented in detail; examples include phonological analogy, over-emphasis, and a host of other social and cognitive factors. Any such bias in copying constitutes a form of selection in language evolution." (Newberry et al., 2017, p. 244)

Not so fast! In our view, this reasoning lumps variation bias together with copying bias. Copying bias occurs when a speaker uses "dived" more often because, for example, they hear a cool group using it to which they want to belong. But if a speaker uses "dived" because they overregularize their verb forms, this is a variation bias. The other possibility is of course that they use "dove" simple because they happened to hear it used more often, which would be unbiased copying caused by drift. Copying bias is a two-step process where the selective step takes place socially, in the environment. By contrast, variation bias occurs before language acts are even made. Both cognitive and social factors can produce developmental constraints. In this case, the cognitive factors seem to be driving the constraining, while in the next case we discuss below both cognitive and social factors constrain language evolution.

Conceptually, variation and copying biases can be distinguished then, but in general both variation biases and copying biases take place in any evolving system. Cognitive features like regularization may be adaptive in the sense that they evolved by natural selection in humans for increased efficiency or learning (Culbertson & Kirby, 2016; Ferdinand et al., 2019; Smith, 2011). But their role in human language production and therefore linguistic development could also mean that they constitute linguistic constraints on language variation.

5 Divergent and convergent evolution

The second case comes from Vanuatu, an archipelago in Melanesia in the South Pacific Ocean with the highest language density per capita in the world. With 64 inhabited islands and 234,000 inhabitants (2009 Census), 138 languages have been recorded (François et al., 2015). As such, it provides an amazingly rich case study for linguistic evolution, having been likened to the Galapagos for biological evolution (Goddard, 2016).

Alex François has done extensive linguistic field work on the islands and works on their evolutionary history. In "Social ecology and language history in the northern Vanuatu linkage: A tale of divergence and convergence" he focuses on a subset of the archipelago, the Northern Torres and Banks Islands with population 9359 and 17 languages (François, 2011, p. 230). His main comparative result is that the languages show exceptional diversity in lexicons and near isomorphism in grammars.

François' account of how and why this is observed invokes the history of the islands, their geography, the social values of the inhabitants, and cognitive demands on language speakers. All of the languages in Vanuatu have a common ancestor in Proto-Oceanic circa 3000 years ago and a more recent Proto-North

Central Vanuatu for the subgroup. Every village on these islands is connected to a few other villages through footpaths or waterways, but none are connected to many of the other ones.

Considering the lexicons first, different dialects have drastically different sound changes even where they share cognate words. When a new variant arises in a village, it must spread throughout this village or else it dies out. If it spreads in this village, then it has the chance to spread to other villages speaking the same language. The new word form then quickly comes into contact with speakers of other languages. Here it has a chance to be borrowed into a new language and the spread can continue.

Within this setting, François argues the drivers of sound change and lexical replacement are the generation of variants and what he calls the “fundamental push for in-group homogeneity” (François, 2011, p. 230). The continual change of individual dialects results not from an urge by the speaker group to be different from other groups, but rather to maintain the integrity of the speaker group. When a popular variant emerges in a dialect, the speakers want to ensure that no splitting of the group occurs. Therefore, variants quickly either die off or become adopted by all. Variants do not spread across the entire archipelago because of the limited contact between groups and also the initial hurdle of a group allowing a variant within it.

Underlying this extreme lexical diversity is an almost equal and opposite grammatical uniformity. Describing the situation as “one grammar with 17 lexicons” would only be a slight exaggeration (François, 2011, p. 224). Structural isomorphism concerns the organization of meaning. Perfectly isomorphic sentences can be put into a one-to-one correspondence in their spoken form where every word has a perfect translation into the other language and word order is preserved, making the sentences perfect translations of each other. They can even share the same polysemies (one word with the same set of multiple meanings). François estimates that the Torres-Banks islands show 80–85% structural isomorphism.

The drivers of this structural similarity include cognitive pressures and social ecology. To begin, everyone on these islands is natively bilingual and every village multilingual because of the marriage practices of men marrying women from distant islands. This imposes structural convergence, François argues, because multilingual speakers in contact will always trend towards merely relabeling their native categories using the morphemes of the new language (François, 2011, p. 225). Even though the languages here all share common ancestors, the convergence is not due to retention of inherited constructions alone (François, 2011, p. 225). The speakers are locked into their grammars due to their multilingual environments.

François’ own evolutionary account fits into a Neo-Darwinian picture where only variation, selection, and migration operate. On his rich telling, we see both selection and drift-leaning ways of telling the story. The selection explanatory strategy would emphasize the role that selection plays in the in-groups to either strongly select for a variant or eliminate it. Structural isomorphism is seen as adaptive to the multilingual cognitive systems of the speakers. The drift explanatory strategy instead would emphasize the role that limited diffusion of variants plays in stopping the spread of novel variants and borrowed words. Drift is used to critique and check the scope of selective explanations for word variability patterns.

From our integrated perspective, the key unasked question is, where are the structural grammatical variants? Why do we not see (more of) them? How do we explain this stasis? The selection and drift explanations both assume that structural variants are produced just as lexical variants are. An untested developmental constraint hypothesis is that these variants are simply very rarely, and perhaps only in particular ways, produced at all. The linguistic developmental systems, especially the brains of the speakers, would fail to produce structural variants because they are constrained by their bi- and multilingual language speaking. This would be a prime example of the role of developmental constraints.

While conceptual progress can be made through clarifying mechanisms and proposing alternative hypotheses, we would also say something about how evidence will decide in favor of the various hypotheses drawing again on evolutionary developmental biology. With developmental constraints now under investigation, linguists must make new observations and experiments. Observational data is important but not usually conclusive in itself. In biology, observing very rare variant phenotypes found in nature can show that a phenotype is accessible and strongly implies that it is selected against. However, the lack of a kind of variant is not itself evidence for constraints on form but could be the result of strong selection against the trait. It would be desirable if we could sample all conversations on Vanuatu's islands and track the generation and relative use of especially grammatical variants. This is the only way we can know in what forms they even exist. But it would not be enough to determine the mechanisms responsible for grammatical stasis, though it would be a good start. Observing few grammatical variants would suggest variation bias but could also result from strong copying bias. For example, a case of copying bias comes from Spanish where both "v" and "b" phonemes are used, but they are not distinguished by Spanish speakers. Only many short-lived grammatical variants would be strong observational evidence for copying bias.

Experimental studies are much more powerful tools for probing which phonemes and constructions are accessible to a population. Alberch proposed a general type of experiment for determining whether absences are due to developmental constraints or are adaptations (Alberch, 1982; Amundson, 1994). In this experiment, selective pressures are removed and the populations are allowed to continue evolving. When the gaps in observed phenotypes remain, they are probably constrained against. When the gaps give way to continuous variation, they are due to selection. In practice, experiments can also be done to try to elicit novel variants. More invasive experiments can also be done to intervene on the developmental systems themselves, this being the main way that developmental biologists learn about their systems. To study linguistic development, controlled manipulation of learning and speaking environments should also be used.¹¹ For example, as seen especially in the Vanuatu case, speakers do not often produce grammatical variations. Linguists should investigate how can we manipulate the speech environment such that people begin to make such variations and the constraints that prevent them from doing so.

¹¹ We are frankly quite ignorant at this point about what existing work in experimental linguistics is relevant to evo-devo linguistics.

6 Conclusions

Linguists using a cultural-evolutionary approach have been working under the assumption that a Neo-Darwinian framework involving selection and drift is sufficient for explaining linguistic change. We have shown that developmental constraints and biases, well-known to evolutionary developmental biologists, are unconsidered relevant alternatives in some paradigmatic studies of linguistic evolution. We have also shown how to extend the conceptual framework for linguistic evolution to include developmental constraints and variation biases. The key is a broadened notion of development that includes all processes that contribute to the generation of linguistic variation at the level of individual speakers.

We hope that evolutionary linguists will reframe and reanalyze familiar cases of linguistic change to distinguish and measure drift, selection, and developmental constraints. We have no interest in developmental constraints turning out to be the best explanation or most important causal factor in any particular cases or in general. This is as ever an empirical question. Our intervention here is meant only to give developmental constraints a seat at the table and be considered. This can only lead to more fruitful and accurate investigations of linguistic change.

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Declarations

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