

Linking evolutionary and ecological theory illuminates non-stationary biodiversity

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Abstract

Whether or not biodiversity dynamics tend toward stable equilibria remains an unsolved question in ecology and evolution with important implications for our understanding of diversity and its conservation. Phylo/population genetic models and macroecological theory represent two primary lenses through which we view biodiversity. While phylo/population genetics provide an averaged view of changes in demography and diversity over timescales of generations to geological epochs, macroecology provides an ahistorical description of commonness and rarity across co-occurring species. Our goal is to combine these two approaches to gain novel insights into the non-equilibrium nature of biodiversity. We help guide near future research with a call for bioinformatic advances and an outline of quantitative predictions made possible by our approach.

1 Non-equilibrium, inference, and theory in ecology and evolution

The idea of an ecological and evolutionary equilibrium has pervaded studies of biodiversity from geological to ecological, and from global to local [1–6]. The consequences of non-equilibrium dynamics for biodiversity are not well understood and the need to understand them comes at a critical time when anthropogenic pressures are forcing biodiversity into states of rapid transition [7]. Non-equilibrial processes could profoundly inform conservation, which are only just beginning to be explored [8].

Biodiversity theories based on assumptions of equilibrium, both mechanistic [3, 5, 6] and statistical [see the Glossary; 4, 9] have found success in predicting ahistorical patterns of diversity such as the species abundance distribution [3, 4, 10] and the species area relationship [3, 4]. These theories assume a macroscopic equilibrium in terms of these coarse-grained metrics, as opposed to focusing on details of species identity [such as in 7], although macroscopic and microscopic approaches are not mutually exclusive. Nonetheless, the equilibrium assumed by these theories is not realistic [11], and many processes, equilibrial and otherwise, can generate the same macroscopic, ahistorical predictions [12].

Tests of equilibrial ecological theory alone will not allow us to identify systems out of equilibrium, nor permit us to pinpoint the mechanistic causes of any non-equilibrial processes. The dynamic natures of evolutionary innovation and landscape change suggest that ecological theory could be greatly enriched by synthesizing its insights with inference from population genetic theory that explicitly accounts for history. This would remedy two shortfalls of equilibrial theory: 1) if theory fits observed ahistorical patterns but the implicit dynamical assumptions were wrong, we would make the wrong conclusion about the equilibrium of the system; 2) if theories do not fit the data we cannot know why unless we have a perspective on the temporal dynamics underlying the generation of those data.

No efforts to date have tackled these challenges. We propose that combining insights from ecological theory and inference of evolutionary and demographic change from genetic data will allow us to understand and predict the consequences of non-equilibrium processes in governing the current and future states of ecological assemblages. The advent of next generation sequencing approaches to biodiversity[13–22] have made unprecedented data available for synthesizing insights from ecological theory and genetics/genomics. However, we need a tool set of bioinformatic methods (Box 2) and meaningful predictions (section 6) grounded in theory to make use of those data. Data will take the form of both standard ecological metrics such as species abundances, as well as summaries of demographic/diversity dynamics inferred from genetics. Theory-based predictions will consist of connecting deviations from ecological theory and regions of parameter space with the dynamic processes inferred from genetics, all aided by new bioinformatic advances. We present the foundation of this tool set here.

What is it good for: metabarcode biodiversity, ecological neutral theory applied to microbial communities [23]

2 Ecological theories and non-equilibrium

Neutral and statistical theories in ecology focus on macroscopic patterns, and equilibrium is presumed to be relevant to those patterns, but not the finer-grained properties of ecosystems. Non-neutral and non-statistical models [e.g., 5, 6] also invoke ideas of equilibrium in their derivation. However, these equilibria focus on the micro-scale details of species interactions and therefore do not fall within our primary focus. Here, we focus explicitly on simple yet predictive theories for their utility as null models, not because of a presumption of their realism.

Our goal throughout is not to validate neutral or statistical theories—quite the opposite, we propose new data dimensions, namely genetics, to help better test alternative hypotheses

against these null theories, thereby gaining insight into what non-neutral and non-statistical mechanisms are at play in systems of interest.

To use these theories as null models, we need a robust measure of goodness of fit. The emerging consensus is that likelihood-based test statistics should be preferred [24]. The “exact test” of Etienne [25] has been extended by Rominger and Merow [26] into a simple z-score which can parsimoniously describe the goodness of fit between theory and pattern. We advocate its use in our proposed framework.

The neutral theory of biodiversity [NTB; 3] assumes that one mechanism—demographic drift—drives community assembly. By presuming that individuals of different species within a trophic level are equivalent in regards to competition or resource use, neutrality avoids the intractability of over parameterization and arrives as an equilibrium prediction when homogeneous stochastic processes of birth, death, speciation and immigration have reached stationarity. Thus neutrality in ecology is analogous to neutral drift in population genetics [3].

Rather than assuming any one mechanism dominates the assembly of populations into a community, statistical theories assume all mechanisms could be valid, but their unique influence has been lost to the enormity of the system and thus the outcome of assembly is a community in statistical equilibrium [4, 9]. These statistical theories are consistent with niche-based equilibria [9, 27] if complicated, individual or population level models were to be upscaled to entire communities. The maximum entropy theory of ecology [METE 4] derives its predictions by condensing the many bits of mechanistic information down into ecological state variables and then mathematically maximizing information entropy conditional on those state variables. METE can predict multiple ahistorical patterns, including distributions of species abundance, body size, spatial aggregation, and trophic links [4, 28], making for a stronger test of theory [29]. However, multiple dynamics can still map to this handful of metrics [12] and while extensive testing often supports METE’s predictions

[4, 10, 30] at single snapshots in time, METE fails to match observed patterns in disturbed and rapidly evolving communities [4, 28]. We cannot know why within the current framework of equilibrium theory testing without adding metrics that capture temporal dynamics.

3 Inferring non-equilibrium dynamics

Unlocking insight into the dynamics underlying community assembly will help us overcome the limitations of analyzing ahistorical patterns with equilibrial theory. While the fossil record could be used for this task, it has limited temporal, spatial, and taxonomic resolution. Here we instead focus on population/phylogenetic insights into rates of change of populations and species because of the detailed characterization of demographic fluctuations, immigration, selection, and speciation they provide. Bridging ecological theory with models from population/phylogenetics has great potential [31–36] that has yet to be fully realized. How we can best link the inferences of change through time from phylo/population genetics with inferences from macroecology depends on what specific insights we can glean from genetic perspectives on demography and diversification.

One of the fundamental tools allowing for complex historical inference with population genetic data is coalescent theory [37, 38]. Coalescent theory allows for model-based estimation of historical parameters such as historical population size fluctuations [39], divergence and/or colonization times [40, 41], migration rates [42], selection [43], and complex patterns of historical population structure [44] and gene flow [45, 46]. This approach can also be put in a multi-species, community context via hierarchical demographic models [47–50], even when only small numbers of genetic loci are sampled from populations [51].

These modeled demographic deviations from neutral demographic equilibrium can also be condensed into multi-species summary statistics. For example, Tajima’s D, which measures the strength of non-equilibrium demography in a single population [see Glossary for more details; 52–55], could be averaged over all populations in a sample.

4 Current efforts to integrate evolution into ecological theory

While quantitatively integrating theory from ecology, population genetics, and phylogenetics has not yet been achieved, efforts so far to synthesize perspectives from evolution and ecology point toward promising directions despite being hindered by one or more general issues: 1) lack of a solid theoretical foundation, 2) inability to distinguish multiple competing alternative hypotheses, 3) lack of comprehensive genetic/genomic data, and 4) lack of bioinformatic approaches to resolve species and their abundances.

Phylogenetic information has been incorporated into studies of the NTB to better understand its ultimate equilibrium [56, 57]. However, kindered phylogenetic reasoning also points out the flaws in the NTB’s presumed equilibrium [11]. Attempts to correct the assumed dynamics of NTB through “protracted speciation” [58] are promising, and while their implications for diversification have been considered [59], these predictions have not been integrated with demographic and phylogeographic approaches [e.g., 40, 41, 44] that have the potential to validate or falsify presumed mechanisms of lineage divergence. Such demographic studies, particularly phylogeographic investigations of past climate change [60, 61], have highlighted the non-equilibrium responses of specific groups to perturbations that must be confronted by ecological theory, but no attempt has been made to scale up these observations to implications at the level of entire communities. The recent growth in joint studies of genetic and species diversity [35, 62, 63] have been useful in linking population genetics with ecological and biogeographic theory. These correlative studies could be bolstered by developing full joint models that link community assembly, historical demography and coalescent-based population genetics combined with next generation sequencing based community analysis approaches.

Studies have also used chronosequences or the fossil record in combination with neutral

and/or statistical theory to investigate changes over geologic time in community assembly mechanisms [28, 64]. While these studies have documented interesting shifts in assembly mechanisms, including departures from equilibrium, likely resulting from evolutionary innovations, understanding exactly how the evolution of innovation is responsible for these departures cannot be achieved without more concerted integration with genetic data.

5 What is needed now

A key limitation of using ahistorical theory to infer dynamic mechanisms is that multiple mechanisms, from simple and equilibrial to complex, can map onto the same ahistorical pattern [29, 65]. This means that even when a theory describes the data well, we do not really know the dynamics that led to that good fit [11].

Quantitatively integrating the dynamics inferred from population and phylogenetic approaches with ahistorical, equilibrial ecological theory can break this many-to-one mapping of mechanism onto prediction and contextualize whether a match between ahistorical pattern and theory truly results from equilibrial dynamics or only falsely appears to. There are two complementary approaches to achieve this integration (both discussed further in Box 2):

- Option 1: using dynamics from genetic inference to predict and understand deviations from ahistorical theories. This amounts to separately fitting ahistorical theory to typical macroecological data, while also fitting population genetic and/or phylogenetic models to genetic data captured for the entire community. Doing so requires substantial bioinformatic advances that would allow the joint capture of genetic or genomic data from entire community samples, while also estimating accurate abundances for each species in those same samples.
- Option 2: building off existing theories, develop new joint models that simultaneously predict macroecological and population genetic patterns. This amounts to building

hierarchical models that take genetic data as input and integrate over all possible community states given explicit models of community assembly and population coalescence. Such a model approach also represents a major bioinformatic challenge.

5.1 What we could gain from this framework

Using our proposed framework, we can finally understand why ahistorical theories fail when they do—is it because of rapid population change, or evolution/long-distance dispersal of novel ecological strategies? We could predict whether a system that obeys the ahistorical predictions of equilibrial ecological theory is in fact undergoing major non-equilibrial evolution. We could better understand and forecast how/if systems out of equilibrium are likely to relax back to equilibrial patterns. With such a framework we could even flip the direction of causal inference and understand ecological drivers of diversification dynamics. This last point bears directly on long-standing debates about the importance of competitive limits on diversification. Competition and limiting similarity have a long history of study as drivers of diversification. This has culminated in ideas of diversity-dependent diversification[2], but lacks a link back to ecological assembly mechanisms. Conclusions about phylogenetic patterns (e.g. diversification slowdowns) would be more believable and robust if combined with population genetic inference (e.g. declining populations) and community patterns (e.g. deviation from equilibrium).

6 Evo-ecological predictions for systems out of equilibrium

The data needed to fully test a non-equilibrial theory of ecology and evolution, synthesizing historical and contemporary biodiversity patterns, are unprecedented in scale and depth. We require knowing the species identities of each individual in a sample as well as infor-

mation on some portion of their genomes such that we can estimate historical demography and diversification. In Box 2 we highlight two promising routes: 1) estimating abundance from targeted capture high throughput sequencing data (i.e. metabarcoding) to be used in ahistorical ecological theory testing, and then separately fitting models of demography and diversification; and 2) jointly estimating the parameters of coupled models of community assembly and community-level population genetics. Assuming these two approaches are within reach (as we demonstrate in Box 2), we now discuss hypotheses to be tested in our non-equilibrium framework.

6.1 Cycles of non-equilibrium

Ecosystems experience regular disturbances which can occur on ecological time-scales, such as primary succession, or evolutionary time scales, such as evolution of novel innovations that lead to new ecosystem processes [66]. We hypothesize that these regular disturbances can lead to cycles of non-equilibrium in observed biodiversity patterns.

Figure 1 derives from comparing summaries of deviation from neutral/statistical equilibrium on the y-axis and deviations from equilibrial demography/diversification on the x-axis. Trajectories of biodiversity assemblages through this space shows how we hypothesize biodiversity to transition between different phases of equilibrium and non-equilibrium. A clockwise cycle through this space would indicate:

- Panel I \rightarrow Panel II: following rapid ecological disturbance, ecological metrics diverge from equilibrium
- Panel II \rightarrow III: ecological non-equilibrium spurs evolutionary non-equilibrium leading to both ecological and evolutionary metrics diverging from equilibrium values
- Panel III \rightarrow IV: ecological relaxation to equilibrium after evolutionary innovations provide the means for populations to re-equilibrate to their environments

- Panel IV \rightarrow I: finally a potential return to equilibrium of both ecological and evolutionary metrics once evolutionary processes have also relaxed to their equilibrium

Cycles could also be much shorter, with a system only transitioning back and forth between Panel I and Panel II. This scenario corresponds to the system being driven only by rapid ecological disturbance, and this disturbance itself following a stationary dynamic leading to no net evolutionary response.

Cycles through this space could also occur in a counterclockwise direction, being initiated by an evolutionary innovation. Under such a scenario we hypothesize the cycle to proceed:

- Panel I \rightarrow IV: non-equilibrium evolution (including sweepstakes dispersal) leading to departure from evolutionary equilibrium before departure from ecological equilibrium
- Panel IV \rightarrow III: non-equilibrium ecological response to non-equilibrium evolutionary innovation
- Panel III \rightarrow I: ecological and evolutionary relaxation

We hypothesize that the final transition will be directly to a joint equilibrium in ecological and evolutionary metrics (Panel I) because a transition from panel III to panel II is unlikely, given that ecological rates are faster than evolutionary rates.

A complete cycle cannot be observed without a time machine, but by combining ahistorical ecological theory and population/phylogenetic inference methods with community-level genetic data we can identify where on the cycle our focal systems are located. Such an approach assumes that abundance data have been estimated from sequence data, ahistorical ecological theories have been fit to those abundance data, and models of population demography and/or diversification have been separately fit to the underlying sequence data. To better understand how our focal systems have transitioned between different equilibrium and non-equilibrium phases, we must more deeply explore the joint inference of community assembly

and evolutionary processes. In the following sections we do just that for each transition shown in Figure 1. We bring to bear other aspects of joint eco-evolutionary inference, in particular the 1) relationship between lineage age (inferred from molecular data) and lineage abundance; 2) the nature of deviation from ecological metrics, specifically the shape of the species abundance distribution; and 3) the nature of deviation from evolutionary metrics, specifically inference of past population change and selection.

6.2 Systems undergoing rapid ecological change

For systems whose metrics conform to demographic predictions of equilibrium, but deviate from equilibrial ecological theory, we predict that rapid ecological change underlies their dynamics. However, more information is needed to confirm that the system is being driven primarily by rapid ecological change. The first line of evidence could come from a lack of correlation between lineage age and lineage abundance—this would indicate that slow eco-evolutionary drift is interrupted by frequent perturbations to populations, making their size independent of age (Fig. 2). Actual abundance should similarly be uncorrelated with inference of effective population size from genetic data. Further support for the ecology-only hypothesis could come from a lack of directional selection detected in community-wide surveys of large genomic regions (see Box 1). Taken as a whole, systems in which ecological metrics deviate from equilibrial theory while demographic and macroevolutionary metrics conform to equilibrial theory presents an opportunity to understand and test hypotheses relating to disturbance, assembly, and the shape of the species abundance distribution [e.g., 4].

6.3 Non-equilibrium ecological communities fostering non-equilibrium evolution

A lack of equilibrium in an ecological assemblage means that the system will experience change on its trajectory toward a future possibility of equilibrium. If ecological relaxation does not occur—by chance, or because no population present is equipped with the adaptations to accommodate the new environment—then the system is open to evolutionary innovation. Such innovation could take the form of elevated speciation or long-distance immigration, relating to the idea that community assembly is a race between processes with potentially different, but stochastic rates [62]. Speciation and sweepstakes immigration/invasion will yield very different phylogenetic signals, however their population genetic signals in a non-equilibrium community may be very similar (e.g. rapid population expansion). Thus where non-equilibrium communities foster non-equilibrium diversification (either through speciation or invasion) we expect to see a negative relationship between lineage age and abundance (Fig. 2).

6.4 Non-equilibrium evolution fostering non-equilibrium ecological dynamics

If evolutionary processes, or their counterpart in the form of sweepstakes immigration/invasion, generate new ecological strategies in a community, this itself constitutes a form of disturbance pushing the system to reorganize (Fig. 1 Panel I to IV to III). Evolutionary change would have to be extremely rapid to force ecological metrics out of equilibrium, thus we would expect to see phylogenetic signals of adaptive radiation, and corresponding signals of strong selection in genomic-scale sequence data.

6.5 Ecological and evolutionary relaxation

Ecological metrics can return to equilibrium either by ecological means or by evolutionary means. In either case, communities are likely to return to equilibrium given enough time without disturbance. Because ecological rates are typically faster than evolutionary rates, this ecological relaxation is likely to happen more quickly than evolutionary relaxation, and thus genetic inference may reveal a time-averaged demographic signature of non-equilibrium. Given sufficient time in ecological equilibrium, this time averaged demographic record revealed by genetic inference will likely also re-equilibrate.

7 Harnessing evo-ecological measures of non-equilibrium for a changing world

Inference of community dynamics needs to expand the dimensions of data it uses to draw conclusions about assembly of biodiversity and whether/when this is an equilibrial or non-equilibrial process. The need for more data dimensions is supported by others [12]; however, accounting for the complexities of history by explicitly linking theories of community assembly with theories of evolutionary genetics is novel, and made possible by advances in:

1. high throughput sequencing (Box 1) that allow genetic samples to be economically and time-effectively produced on unprecedented scales
2. bioinformatic methods (Box 2) that allow us to make sense of these massive community-wide genetic/genomic datasets
3. theory development (section 6) that provides meaningful predictions to test our new bioinformatic approaches

This approach is a fertile cross pollination of two fields that, while successful in their

own right, are enhanced by their integration. While comparative historical demographic models are advancing [47–50], testing community-scale hypotheses with multi-taxa data would be profoundly improved and enriched if population genetic model were grounded in macroecological and biogeographic theory. What is more, it has been long recognized that models in community ecology have been overly reliant on ahistorical patterns, such as the species abundance distribution, which are by themselves often insufficient for distinguishing competing models of assembly [12]. The field is ready to fully merge these two approaches using the wet lab, bioinformatic, and theoretical-conceptual approaches we have promoted here . This time to do so is now, as scientists face an increasingly non-equilibrium world and its consequences for our fundamental understanding of what forces govern the diversity of life and how we can best harmonize human activities with it.

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Boxes

Box 1: Wetlab techniques

Next generation sequencing technology has ushered in a revolution in evolutionary biology and ecology. The large scale recovery from bulk samples (e.g. passive arthropod traps) of species richness, food web structure, and cryptic species promise unprecedented new insights into ecosystem function and assembly [13–15, 67]. Two approaches, differing in cost and effectiveness, have emerged.

Metabarcoding describes the targeted PCR amplification and next generation sequencing of short DNA barcode markers (typically 300-500 bp) from community samples [16]. The resulting amplicon sequences can be clustered into OTUs or grafted onto more well supported phylogenies. Even minute traces of taxa in environmental samples can be detected using metabarcoding [18]. Amplicon sequencing is cheap, requires a small workload, and thus allows rapid inventories of species composition and species interactions in whole ecosystems [14, 20]. However, the preferential amplification of some taxa during PCR leads to highly skewed abundance estimates [68] from metabarcoding libraries.

Metagenomic approaches, in contrast, avoid marker specific amplification bias by sequencing libraries constructed either from untreated genomic DNA [19, 21], or after targeted enrichment of genomic regions [22]. While being more laborious, expensive and computationally demanding than metabarcoding, metagenomics thus offers improved accuracy in detecting species composition [17]. Moreover, the assembly of high coverage metagenomic datasets recovers large contiguous sequence stretches, even from rare members in a community, offering high phylogenetic resolution at the whole community level [69]. Due to large genome sizes and high genomic complexity, metazoan metagenomics is currently mostly limited to the assembly of fairly short high copy regions. Particularly mitochondrial and

chloroplast genomes as well as nuclear ribosomal clusters are popular targets [21, 69]. In contrast, microbial metagenomic studies now routinely assemble complete genomes and characterize gene content and metabolic pathways even from complex communities [70]. This allows unprecedented insights into functional genetic process underlying community assembly and evolutionary change of communities to environmental stress. Such whole genome based community analysis is not yet feasible for macroorganisms. However, considering the ever increasing throughput and read length of next generation sequencing technology, as well as growing number of whole genomes, it might well become a possibility in the near future, opening up unprecedented new research avenues for community ecology and evolution.

Box 2: Bioinformatic advances

While species richness can be routinely identified by sequencing bulk samples using high throughput methods, estimating species abundance remains challenging [68] and severely limits the application of high throughput sequencing methods to many community-level studies. We propose two complementary approaches to estimate species abundance from high throughput data. The first approach estimates abundance free from any models of community assembly, the second jointly estimates the parameters of a specific assembly model of interest along with the parameters of a coalescent-based population genetic model.

Model-free abundance estimation. We propose a pipeline (Fig. 1) where raw reads are generated and assembled into a phylogeny using standard approaches, and potentially aided by additionally available sequence data in a super tree or super matrix approach. The numbers of sequences assigned to each terminal tip are then used in a Bayesian hierarchical model which seeks to estimate the true number of organisms representing each terminal tip, accounting for sequencing biases originating from, e.g. primer affinity and copy number differences between taxa. Information on phylogenetic relatedness can inform modeled correlations in biases between taxa [71, e.g. copy number is known to be phylogenetically

conserved at least in microbes]. This approach is particularly tailored to metabarcoding data. In a potentially powerful extension, and thanks to the proposed Bayesian framework, information from sequencing experiments that seek to calibrate metabarcoding studies [e.g., 67] can be used to build meaningfully informative priors and improve model accuracy. Through a simulation study (described in the supplement) we show that true underlying abundances can be accurately estimated (Fig. II).

Joint inference of community assembly and population genetic models. Coupling individual-based, forward-time models of community assembly with backwards-time hierarchical multi-taxa coalescent models permits inference about the values of the parameters in both models. This framework is flexible enough to incorporate multiple refugia, colonization routes, ongoing migration and both neutral and deterministic processes of assembly on time scales of hundreds of thousands of years (Fig. III). A forthcoming implementation [gimmeSAD π ; 72] simulates an individual-based forward time community dispersal model [73] linked with the msPrime coalescent simulator [74]. This has been accomplished by rescaling the time dependent local abundance distributions into time dependent effective population size distributions while allowing for heterogeneity in migration and colonization rates. This simulation model can be combined with random forest classifiers and hierarchical ABC to enable testing alternative assembly models, including models that have not yet reached their theoretical equilibria.

Glossary

ahistorical Patterns or theories which do not contain information about the historical processes that gave rise to them

Approximate Bayesian computation (ABC) . A method of calculating an approximate posterior sample of parameters in a complex model whose likelihood function cannot

be analytically solved by simulating realizations of the model, computing summary statistics from those realizations, and probabilistically accepting or rejecting the parameter values leading to those summary statistics based on their agreement with the observed statistics computed from the real data.

coalescent A backwards in time model approach in population genetics in which alleles in the sample are traced to their ancestors under demographic models of interest.

equilibrium Equilibrium is often reserved for systems in thermodynamic equilibrium—which all life violates. By “biodiversity equilibrium” we make an analogy to thermodynamics and say that biodiversity is in equilibrium if its macroscopic state (e.g. richness of species abundance distribution, but not necessarily specific species compositions) is steady, and across arbitrary subsystems, the same steady state applies.

hierarchical model A modeling approach that facilitates complex hypotheses and causal relationships by allowing model parameters at one level to be dependent on parameters at another level.

statistical equilibrium In the context of biodiversity, a description of a steady state arrived at not by the force of one or a few deterministic mechanisms but by the stationary, statistical behavior of very large collections of mechanistic drivers acting on large assemblages of organisms.

Tajima’s D A metric of non-stationary evolution computed as the difference between two distinct derivations of theoretical genetic diversity. If neutral molecular evolution in a constant population holds, both derivations should be equal, and otherwise if assumptions of constant demography and neutral selection are violated, will be unequal.

Outstanding Questions

1. Can we learn by synthesizing macroecological and population genetic theory whether observed non-equilibrium states are driven by natural disturbance regimes or by anthropogenic forces?
2. Can we learn the relative roles of evolutionary processes (speciation, extinction) vs. successional processes (driven by, e.g., competition, mutualisms, dispersal) as drivers of non-equilibrium macroecology?
3. How can functional genomics be used to better distinguish between purely demographic and niche-based drivers of non-equilibrium? Can understanding the functional content of genomes across taxa in a community help predict potential for non-equilibrium responses to future perturbations? Functional genomics is still very much in development (see Box 1), but future prospects are exciting.
4. How can relative abundance data derived from ancient DNA and fossil data be leveraged within a joint model that generates predictions of spatiotemporal distributions of genetic polymorphism and species abundances? One such opportunity is the availability of highly resolved estimates of relative abundance distributions of forest tree assemblages that are derived from paleo-pollen data [75] which could allow for joint inference in conjunction with assemblage-level genomic sampling. Likewise, obtaining community-level DNA preserved in lake sediments sampled at different late Pleistocene and Holocene could provide for a whole new lense for testing models that account for historical dynamics at both evolutionary and ecological time scales [76].

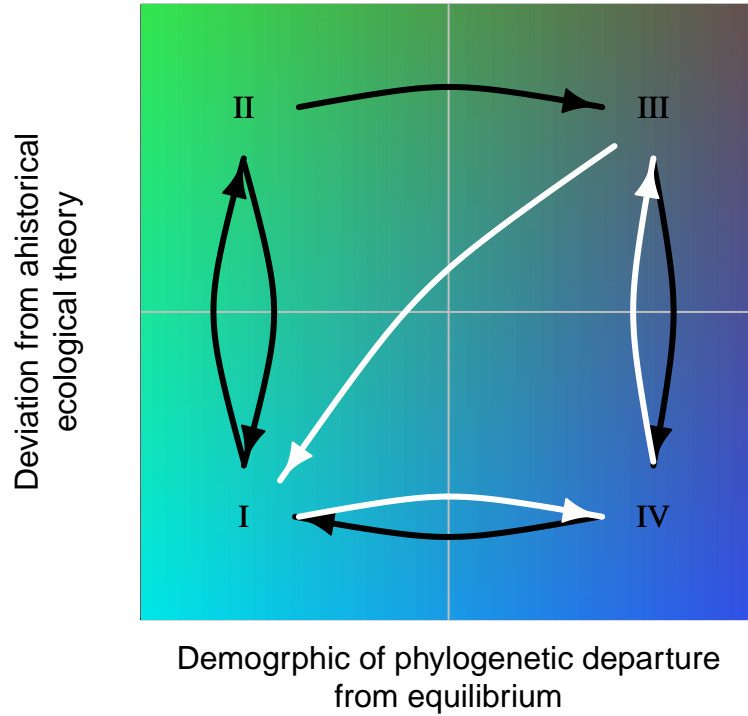


Figure 1: Hypothesized cycles between different states of equilibrium and non-equilibrium in ecological theory (y-axis) and evolutionary demography/diversification (x-axis). Deviations from ecological theory can be quantified by the previously discussed exact tests [25] and z-scores [26], while many statistics are available to quantify departure from demographic/diversification steady state including the previously discussed Tajima's D. Panels I–IV are discussed in the text. Colors correspond to deviation from ahistorical ecological theory and evolutionary equilibrium. Black cycle corresponds to non-equilibrium initiated by ecological disturbance (with potential to continue to evolutionary non-equilibrium or relaxation to equilibrium). White cycle is initiated by evolutionary innovation.

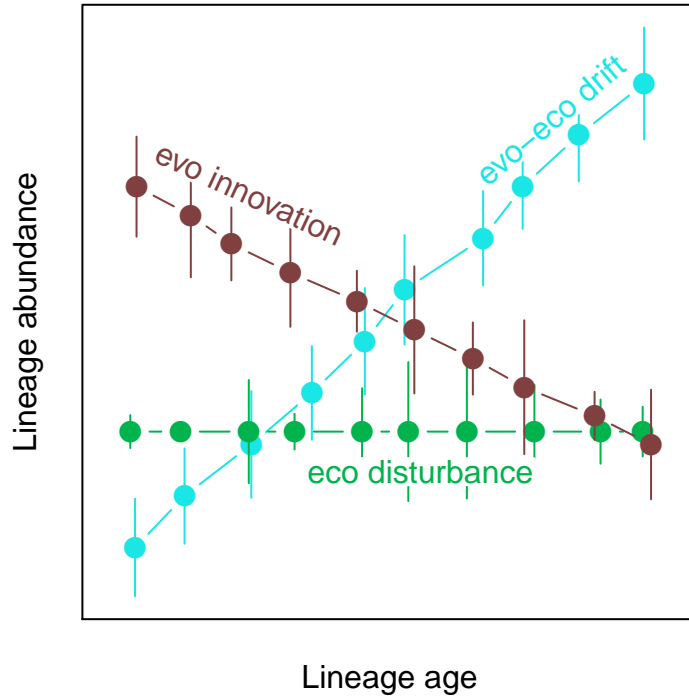


Figure 2: Hypothesized relationships between lineage age and abundance under different evo-ecological scenarios. Colors correspond to panels in Figure 1: teal is evo-ecological equilibrium; green is rapid transition to ecological non-equilibrium following short timescale disturbance; dark brown is non-equilibrium in both ecological and evolutionary metrics.

596 **Box 2** figures

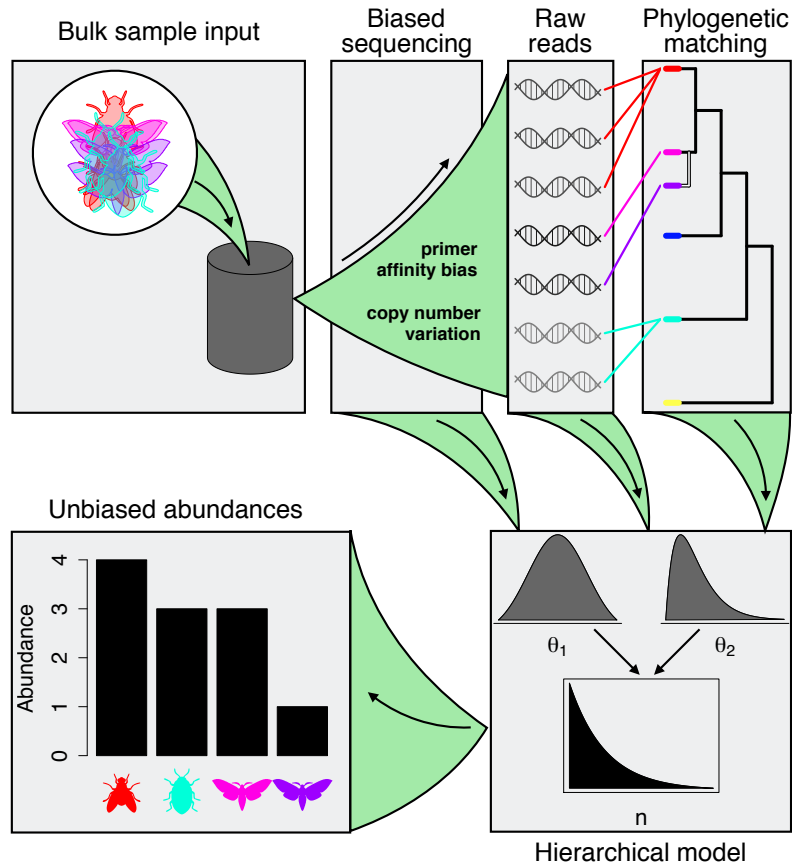


Figure I: Pipeline to estimate true abundances from metabarcoding data. The pipeline follows sequence generation, matching sequences to a phylogeny (generated from the sequences themselves, or better yet from higher coverage data) and finally Bayesian hierarchical modeling leading to abundance estimates.

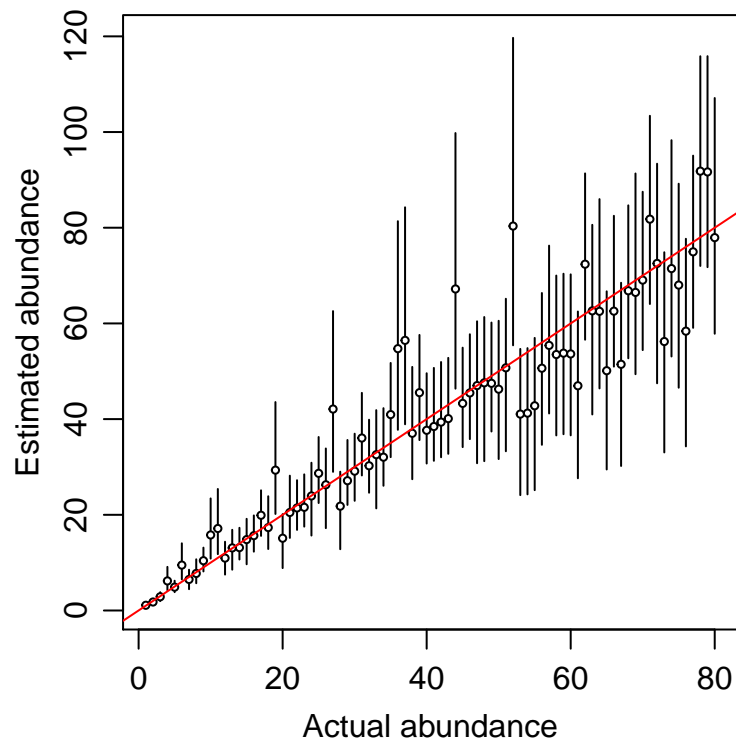


Figure II: Demonstration of agreement between actual and estimated abundances. Actual (simulated) abundances are on the x-axis, which the y-axis shows estimated abundances (error bars are 95% maximum credible intervals). The simulation study is described in the supplement.

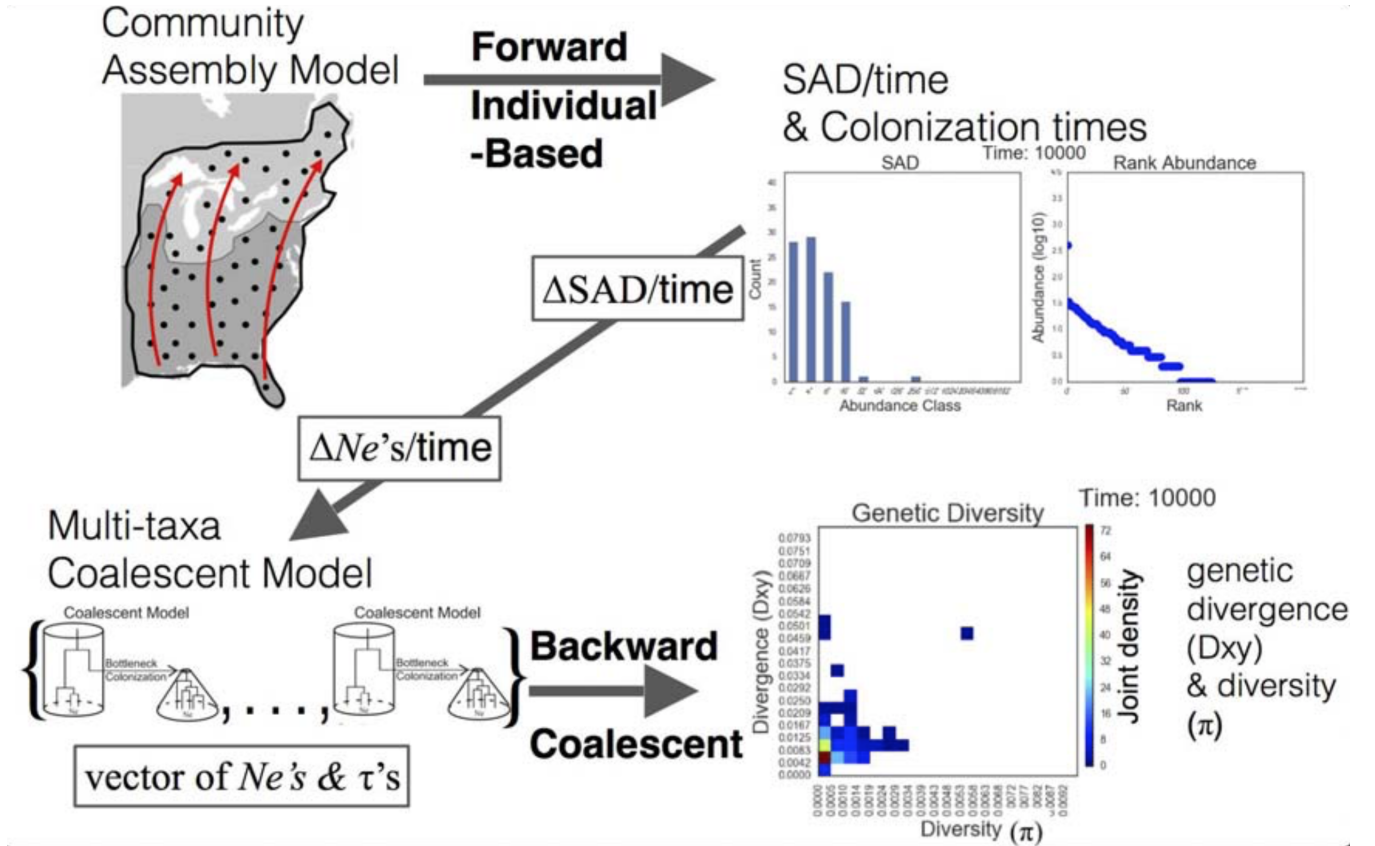


Figure III: The gimmeSAD π pipeline. The forward time models involves multi-regional expansion generating local abundance distributions over time with heterogeneity in colonization times. These temporally dynamic local abundances are re-scaled into local n_e distributions over time to generate multi-species genetic data the the coalescent, which is summarized here with a time-dependent joint spectrum of genetic diversity statistics.