# Outline

1. As biologists, we are tasked with understanding and predicting how ecological/evolutionary systems change over time, especially in an era of dramatic changes to biodiversity.
2. Enormity-of-the-system/statistical equilibrium argument for focusing on deviations from statistical null models
3. Efforts to apply this approach in ecology have been intriguing, but constrained by 1) too few comparison/evaluation points 2) the scarcity of *historical* data
4. Incorporating population genetics with ecological patterns would 1) provide an additional point for inference and 2) *specifically* a point of inference that encodes information about past dynamics.
5. This approach shows promise but has been constrained by 1) a lack of quantitative theoretical work integrating null models of popgen and ecology, 2) a lack of widely-available joint community genetics-and-abundance data to ground theoretical work.
6. Both of these are addressed by recent advances: 1) the double-neutral line of MESS thinking and 2) wetlab and bioinformatic technologies for NGS.
7. Here we illustrate how joint neutral modeling of popgen and ecological dynamics can illuminate the past and future trajectories of eco-evolutionary systems as they move away from and towards macroscopic equilibrium.
   1. Present a theoretical framework for interpreting deviations from macroscopic equilibrium
   2. Simulations demonstrating how specific scenarios map on to the expectations of this framework
   3. Demonstration of bioinformatic advances for plugging real-world data into this framework
8. Call for continued work/signaling of next steps using community genetics data and double-neutral modeling to understand and predict trajectories of eco-evolutionary change.

# Outline with paragraphs mapped back on

1. As biologists, we are tasked with understanding and predicting how ecological/evolutionary systems change over time, especially in an era of dramatic changes to biodiversity.
   1. The consequences of non-equilibrium dynamics for biodiversity are not well understood and the need to understand them is critical with anthropogenic pressures forcing biodiversity into states of rapid transition [(Blonder et al., 2015)](https://paperpile.com/c/Pd4sgd/i1NY). Non-equilibrial processes could profoundly inform conservation in ways only just beginning to be explored [(Wallington et al., 2005)](https://paperpile.com/c/Pd4sgd/VwYi).
2. Enormity-of-the-system/statistical equilibrium argument for statistical null models
   1. **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 marcrosopic 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.
   2. **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.
   3. Neutral and statistical theories in ecology focus on macroscopic patterns, and equilibrium is presumed to be relevant to those patterns. 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.
   4. The unified neutral theory of biodiversity (UNTB; [(Hubbell, 2001)](https://paperpile.com/c/Pd4sgd/MSGg)) is a useful null because it assumes that one mechanism—demographic drift—drives community assembly. Equilibrium occurs 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 [(Hubbell, 2001)](https://paperpile.com/c/Pd4sgd/MSGg).
   5. 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 influences have been lost to the enormity of the system and thus the outcome of assembly is a community in statistical equilibrium [(Harte, 2011; Pueyo et al., 2007)](https://paperpile.com/c/Pd4sgd/Aw1z+pN8k). The mechanistic agnosticism is what makes statistical theories useful nulls. These statistical theories are also consistent with niche-based equilibria [(Neill et al., 2009; Pueyo et al., 2007)](https://paperpile.com/c/Pd4sgd/pN8k+sOe4) if the complicated, individual or population level models with many mechanistic drivers were to be upscaled to entire communities.
3. Efforts to apply this approach in ecology have been intriguing, but constrained by 1) too few comparison/evaluation points 2) the scarcity of *historical* data
   1. The maximum entropy theory of ecology (METE; [(Harte, 2011)](https://paperpile.com/c/Pd4sgd/Aw1z)) 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 [(Harte, 2011; Rominger et al., 2016; Rominger & Merow, 2017)](https://paperpile.com/c/Pd4sgd/Aw1z+7LLQ+rECw), making for a stronger null theory [(B. McGill, 2003)](https://paperpile.com/c/Pd4sgd/KsTJ). However, multiple dynamics can still map to this handful of metrics [(B. J. McGill et al., 2007)](https://paperpile.com/c/Pd4sgd/bWIQ) and while extensive testing often supports METE’s predictions [(Harte, 2011; White et al., 2012; Xiao et al., 2015)](https://paperpile.com/c/Pd4sgd/Aw1z+mCMa+Qx1h) at single snapshots in time, METE fails to match observed patterns in disturbed and rapidly evolving communities [(Harte, 2011; Rominger et al., 2016)](https://paperpile.com/c/Pd4sgd/7LLQ+Aw1z). Just like deviations from UNTB, we cannot know the cause of these departures from theoretical predictions without adding tests of theories and metrics that capture temporal dynamics.
   2. Biodiversity theories based on assumptions of equilibrium, both mechanistic [(Chesson, 2003; Hubbell, 2001; Tilman, 2004)](https://paperpile.com/c/Pd4sgd/0Wfq+MSGg+3E3z) and statistical **(see the Glossary)** [(Harte, 2011; Pueyo et al., 2007)](https://paperpile.com/c/Pd4sgd/pN8k+Aw1z) have found success in predicting ahistorical patterns of diversity such as the species abundance distribution [(Harte, 2011; Hubbell, 2001; White et al., 2012)](https://paperpile.com/c/Pd4sgd/MSGg+Aw1z+mCMa) and the species area relationship [(Harte, 2011; Hubbell, 2001)](https://paperpile.com/c/Pd4sgd/MSGg+Aw1z). 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 [(Blonder et al., 2015)](https://paperpile.com/c/Pd4sgd/i1NY)), although macroscopic and microscopic approaches are not mutually exclusive. Nonetheless, the equilibrium assumed by these theories is not realistic [(Ricklefs, 2006)](https://paperpile.com/c/Pd4sgd/Nsck), and many processes, equilibrial or otherwise, can generate the same macroscopic, ahistorical predictions [(B. J. McGill et al., 2007)](https://paperpile.com/c/Pd4sgd/bWIQ).
   3. 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 those data.
4. Incorporating population genetics with ecological patterns would 1) provide an additional point for inference and 2) *specifically* a point of inference that encodes information about past dynamics.
   1. Unlocking insight into the dynamics underlying community assembly is key to overcoming 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 while there are real limitations in the accuracy and resolution of temporal dynamics with population genetic (cite) and phylogenetic (cite) methods, they can, in principle, be applied to any extant group. Additionally, despite limitations in resolving detailed temporal dynamics, robust metrics of deviation from simple, stationary birth-death and/or speciation-extinction processes have been well-established and widely used for population genetic and phylogenetic data (cite about Tajima D, gamma stats, etc).
   2. Bridging ecological theory with models from population/phylogenetics has great potential [(Dexter et al., 2012; Laroche et al., 2015; Lavergne et al., 2010; McGaughran, 2015; Papadopoulou et al., 2011; Webb et al., 2002)](https://paperpile.com/c/Pd4sgd/Uqik+3qsP+SvCv+Qx5i+xR01+PPJL) that has yet to be fully realized. How we can best link the inferences of change through time from population/phylogenetics with inferences from macroecology is governed by what insights we can gain from genetic perspectives on demography and diversification. Coalescent theory [(Kingman, 1982; Rosenberg & Nordborg, 2002)](https://paperpile.com/c/Pd4sgd/pFWa+2CJb) is one of the fundamental population genetics tools allowing model-based estimation of complex historical processes. These include population size fluctuations [(Kuhner et al., 1998)](https://paperpile.com/c/Pd4sgd/iTVJ), divergence and/or colonization times [(Charlesworth, 2010; Edwards & Beerli, 2000)](https://paperpile.com/c/Pd4sgd/p1Y2+WPtp), migration rates [42], selection [(Kern & Schrider, 2016)](https://paperpile.com/c/Pd4sgd/Ysg8), and complex patterns of historical population structure [(Prado-Martinez et al., 2013)](https://paperpile.com/c/Pd4sgd/POX2) and gene flow [(Beerli & Felsenstein, 2001; Hey & Nielsen, 2004)](https://paperpile.com/c/Pd4sgd/Jx2l+ipvu). This approach can also be put in a multi-species, community context via hierarchical demographic models [(Carstens et al., 2016; Chan et al., 2014; Hickerson et al., 2006; Xue & Hickerson, 2015)](https://paperpile.com/c/Pd4sgd/8dM4+bz82+EbtY+X1Bp), even when only small numbers of genetic loci are sampled from populations [(Drummond et al., 2005)](https://paperpile.com/c/Pd4sgd/J2mW). 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; [(Jensen et al., 2005; Schrider et al., 2016; Stephan, 2016; Tajima, 1989)](https://paperpile.com/c/Pd4sgd/YP6t+pSlH+2mLs+4qbz)], could be averaged over all populations in a sample.
5. This approach shows promise but has been constrained by 1) a lack of quantitative theoretical work integrating null models of popgen and ecology, 2) a lack of widely-available joint community genetics-and-abundance data to ground theoretical work.
   1. While quantitatively integrating theory from ecology, population genetics, and phylogenetics has not yet been achieved, existing efforts 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 with high throughput sequencing data.
   2. Phylogenetic information has been incorporated into studies of the UNTB to better understand its ultimate equilibrium [(Burbrink et al., 2015; Jabot & Chave, 2009)](https://paperpile.com/c/Pd4sgd/zFmb+qFfd). However, phylogenetic reasoning also points out the flaws in the UNTB’s presumed equilibrium [(Ricklefs, 2006)](https://paperpile.com/c/Pd4sgd/Nsck). Attempts to correct the assumed dynamics of UNTB through “protracted speciation” [(Rosindell et al., 2010)](https://paperpile.com/c/Pd4sgd/ifMp) are promising, and while their implications for diversification have been considered [(Etienne & Rosindell, 2012)](https://paperpile.com/c/Pd4sgd/oOFm), these predictions have not been integrated with demographic and phylogeographic approaches (e.g., [(Charlesworth, 2010; Edwards & Beerli, 2000; Prado-Martinez et al., 2013)](https://paperpile.com/c/Pd4sgd/WPtp+p1Y2+POX2)) that have the potential to validate or falsify presumed mechanisms of lineage divergence. Such demographic studies, particularly phylogeographic investigations of past climate change, have highlighted the non-equilibrium responses of specific groups to perturbations [(Hickerson & Cunningham, 2005)](https://paperpile.com/c/Pd4sgd/JmNJ), 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 [(Papadopoulou et al., 2011; Vellend, 2005)](https://paperpile.com/c/Pd4sgd/iKsP+xR01) have been useful in linking population genetics with ecological and biogeographic concepts.
   3. 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 [(Rominger et al., 2016; Wagner et al., 2006)](https://paperpile.com/c/Pd4sgd/ve5v+7LLQ). 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 insights from evolutionary theory.
6. Both of these are addressed by recent advances: 1) the double-neutral line of MESS thinking and 2) wetlab and bioinformatic technologies for NGS.
   1. 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-equilibrial processes in governing the current and future states of ecological assemblages. The advent of high throughput sequencing-enabled metabarcoding has made unprecedented data available about the biodiversity of lineages from microbes to arthropods [(Bohmann et al., 2014; Dodsworth, 2015; Gibson et al., 2014; Ji et al., 2013; Leray & Knowlton, 2015; Linard et al., 2015; Liu et al., 2016; Shokralla et al., 2015; Taberlet et al., 2012; Venkataraman et al., 2015; Zhou et al., 2013)](https://paperpile.com/c/Pd4sgd/scJr+JP9K+XnET+XJha+qjhF+cDwM+XV1c+F7Fb+TOfV+ZkG7+qysb). These metabarcoding data have great potential to yield synthetic insight across ecology and evolution. However, to draw such insights we need a new tool set of bioinformatic methods **(Box box:dry)** and meaningful predictions **(section ref sec:pred )** grounded in theory to make use of those data. We present the foundation of this methedological tool set here.
   2. 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 form equilibrial dynamics or only falsely appears to.
   3. 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 that could lead to these genetic data given a model of community assembly and a model of population coalescence. This approach requires making assumptions about how abundances scale to effective population sizes, but is better suited for comparing competing joint models of evolutionary history and assembly.
   4. We propose a simple yet powerful way to summarize joint inference into deviations from ecological and evolutionary/demographic equilibrium. Assuming that equilibrial models have been independently or jointly fit (Box 2) to a dataset of macroecological metrics (such as species abundances) and genetic/genomic variables (such as community-wide polymorphism data) we can then contrast the system’s deviation from ecological equilibrium with its deviation from evolutionary/demographic equilibrium (Fig. 1). Ecological deviations can be measured by, e.g., the previously discussed z-score [(Rominger & Merow, 2017)](https://paperpile.com/c/Pd4sgd/rECw), while evolutionary/demographic deviations can be captured by summary statistics such as community-averaged Tajima’s D. The space of equilibrium and non-equilibrium states that this comparison generates (Fig. 1) can be used to understand a communities current state, and predict its past and future. Additional predictions from joint eco-evolutionary inference can be tested to further understand a systems’ trajectory through phases of equilibrium and non-equilibrium. One particularly useful metric is the relationship between lineage age (colonization or divergence time inferred from molecular data) and lineage abundance (Fig. 2), which is known to be a telling test of the NTB [(Ricklefs, 2006; Rosindell et al., 2010)](https://paperpile.com/c/Pd4sgd/Nsck+ifMp). Competing different models of assembly and coalescence in a model selection framework can also provide insight.
7. Here we illustrate how joint neutral modeling of popgen and ecological dynamics can illuminate the past and future trajectories of eco-evolutionary systems as they move away from and towards macroscopic equilibrium.
   1. Present a theoretical framework for interpreting deviations from macroscopic equilibrium
      1. Everything under Cycles of nonequilibrium; Figure 1: <https://docs.google.com/document/d/1uD0m2FvLvSrAOrp9QwaNWK9Io2XY8Qz5arRvhegBAxY/edit#bookmark=id.gnh8ufd40y8n>
   2. Simulations demonstrating how specific scenarios map on to the expectations of this framework
      1. New results/perturbations “sampling platter”
   3. Demonstration of bioinformatic advances for plugging real-world data into this framework
      1. Box 2, Box 2 Figure 2, proof-of-concept simulations: <https://docs.google.com/document/d/1uD0m2FvLvSrAOrp9QwaNWK9Io2XY8Qz5arRvhegBAxY/edit#bookmark=id.xma38cnlzcdt>
8. Call for continued work/signaling of next steps using community genetics data and double-neutral modeling to understand and predict trajectories of ecoevolutionary change.

**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 [(Erwin, 2008)](https://paperpile.com/c/Pd4sgd/wAjz). We hypothesize that these regular disturbances can lead to cycles of non-equilibrium in observed biodiversity patterns. Using the phase space of equilibrium and non-equilibrium states showing in Figure 1 a clockwise cycle through this space would indicate:

* Panel I → II: following rapid ecological disturbance, ecological metrics diverge from equilibrium. The system could potentially relax back to equilibrium (Panel II → Panel I), indicating a stationary disturbance process that has no net evolutionary consequences. Conversely,
* Panel II → III: ecological non-equilibrium spurs evolutionary non-equilibrium leading to both ecological and evolutionary metrics diverging from equilibrium values
* Panel III → IV: evolutionary innovations provide the means for ecological processes to re-equilibrate to their environments
* Panel IV → I: finally a potential return to equilibrium on both ecological and evolutionary time scales once evolutionary processes have also relaxed.

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 → IV: non-equilibrium evolution (including sweepstakes dispersal) leading to departure from evolutionary equilibrium before departure from ecological equilibrium
* Panel IV → III: non-equilibrial ecological response to non-equilibrium evolutionary innovation
* Panel III → 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 rate are faster than evolutionary rates. In general these cycles can be combined arbitrarily depending on the forces and dynamics present in the system. However, transitions where evolutionary rates must opperate faster than ecological rates (i.e. Panel III → II and Panel IV → Panel II) are less likely.

A complete cycle cannot be observed without a time machine, but by combining ahistorical ecological theory and population/phylogenetic inference methods using community-level genetic data we can identify where in this space our focal systems are located. To determine their trajectory through this space we must more deeply explore the joint inference of community assembly and evolutionary processes. In the following sections we do that for each transition shown in Figure 1 using patterns of lineage age and abundance together with model selection.

**Systems undergoing rapid ecological change**

For systems whose metrics conform to demographic equilibrium, but deviate from equilibrial ecological theory (Panel I → II), a lack of correlation between lineage age and lineage abundance would indicate that rapid ecological change underlies their dynamics. If slow, equilibrial evolutionary drift is punctuated by regular ecological perturbations, population size would be independent of age (Fig. 2). Actual abundance should similarly be uncorrelated with effective population size in joint genetic-assembly models.

**Ecological relaxation**

Ecological relaxation occurs when populations return to steady state. Both ecological (Panel II → I) and evolutionary (Panel III → IV) mechanisms can facilitate this process (e.g. changes in local population sizes following environmental change [7], or evolution of new species interactions such as host switching [(Rominger et al., 2016)](https://paperpile.com/c/Pd4sgd/7LLQ)). If ecological mechanisms are responsible, age and abundance should again be uncorrelated; if evolutionary mechanics are responsible, age and abundance should be negatively correlated (Fig. 2).

**Non-equilibrium ecological communities fostering nonequilibrium evolution**

A lack of equilibrium in an ecological assemblage means that the system will likely experience change in order to re-equilibrate. 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 (Panel II → III). Such innovation could take the form of elevated speciation or long-distance immigration. 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). Similarly, in a joint genetic-assembly modeling framework, population expansion models should be favored over demographically stationary models.

**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 (Panel IV → III). Evolutionary change would have to be extremely rapid to force ecological metrics out of equilibrium, thus in this scenario we would expect a negative correlation between age and abundance (Fig. 2) and model selection favoring joint genetic-assembly models with highly structured populations and rapid divergence rates. If data become available for large regions of genomes for entire communities, signals of strong selection could also validate non-equilibrium evolution fostering non-equilibrium ecological dynamics (see Outstanding Questions).

**Evolutionary relaxation**

Evolutionary demographic models average over timescales determined by generation time, population size and mutation/selection balance [(Kingman, 1982; Rosenberg & Nordborg, 2002)](https://paperpile.com/c/Pd4sgd/pFWa+2CJb). Evolutionary relaxation (Panel III 8 → I or IV → I) means this time-averaged history returns to stationarity, which can occur if perturbations are absent, or occur on rapid enough time scales (i.e. Panel II → I) to be averaged over. By definition, if a system is found in evolutionary demographic equilibrium it has forgotten any non-equilibrium phases in its history. Thus to detect this kind of long-term relaxation we need data from the fossil record (see Outstanding Questions).

**Box 2: Bioinformatic advances**

While species richness can be routinely identified by sequencing bulk samples using high throughput methods, estimating species abundance remains challenging [(Elbrecht & Leese, 2015)](https://paperpile.com/c/Pd4sgd/rr9A) 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. I) 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 [(Angly et al., 2014)](https://paperpile.com/c/Pd4sgd/rxEt); 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., [(Krehenwinkel et al., 2017)](https://paperpile.com/c/Pd4sgd/N0G7)) 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 [(Overcast et al., 2019, 2021)](https://paperpile.com/c/Pd4sgd/Na77+DU7W) jointly models a forward-time individual-based neutral community assembly process [(Rosindell et al., 2015)](https://paperpile.com/c/Pd4sgd/eUlF) and corresponding expectations of community level genetic diversity and divergence using the msPrime coalescent simulator [(Kelleher et al., 2016)](https://paperpile.com/c/Pd4sgd/u4p3). 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.