

SYNTHESIS



Integrating systematics and biogeography to disentangle the roles of history and ecology in biotic assembly

Brian C. Weeks^{1,2*}, Santiago Claramunt² and Joel Cracraft²

¹Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, USA, ²Department of Ornithology, American Museum of Natural History, New York, NY, USA

ABSTRACT

Aim We develop a conceptual framework for integrating evolutionary history and ecological processes into studies of biotic assembly.

Location Global.

Methods We use theoretical and empirical examples to demonstrate that species distributions are non-random outcomes of first-order processes of biotic evolution: allopatry (isolation of populations), speciation and dispersion of biotas across landscapes. We then outline generalizable steps for integrating methods of phylogenetic and historical biogeographical analyses into studies of biotic assembly.

Results We present a framework that can be applied to any biotic assemblage amenable to phylogenetic and historical biogeographical analyses, can accommodate changes in spatial extent and temporal scale, and will facilitate comparison of assembly processes across biotas. Additionally, we demonstrate the utility of an historical approach for providing context to ecological influences on evolutionary processes, such as trait evolution.

Main conclusions By focusing on reconstructing the histories of individual lineages, an historical approach to assembly analysis can reveal the timing and underlying processes guiding biotic assembly, making it possible to disentangle the roles of history and ecology in the assembly process.

Keywords

community assembly, community phylogenetics, competitive exclusion, habitat filtering, historical biogeography, phylogenetic clustering, phylogenetic overdispersion, regional species pool, trait evolution

*Correspondence: Brian Weeks, Department of Ecology, Evolution and Environmental Biology, Columbia University, 1200 Amsterdam Avenue, New York, NY 10027, USA.
E-mail: bcw2115@columbia.edu

INTRODUCTION

The information contained in the evolutionary relationships of co-occurring species has the potential to illuminate the processes underlying biotic assembly (Elton, 1946; Diamond, 1975; Webb *et al.*, 2002; Vamosi *et al.*, 2009). In recent years, there have been advances in methods that search for patterns in the phylogenetic relationships among co-occurring species. Interpretations of these patterns have led to the development of the field of community phylogenetics (Webb *et al.*, 2002; Johnson & Stinchcombe, 2007; Cavendar-Bares *et al.*, 2009; Vamosi *et al.*, 2009; Vellend, 2010). Community phylogenetic studies have focused primarily on the roles of biotic interactions (e.g. competition and predation) and abiotic filters as the causal bases for structuring taxonomic

composition (Gleason, 1926; Diamond, 1975; Weiher & Keddy, 1999; Hubbell, 2001; Gotzenberger *et al.*, 2012, and references therein).

Multiple approaches exist for integrating phylogenetic data and species distributions to examine patterns of co-occurrence (Webb *et al.*, 2002; Johnson & Stinchcombe, 2007; Kraft *et al.*, 2007; Emerson & Gillespie, 2008; Cavendar-Bares *et al.*, 2009; Kembel, 2009; Vamosi *et al.*, 2009; Vellend, 2010; Swenson, 2013; Borregaard *et al.*, 2014; Pigot & Etienne, 2015). Increasingly, these approaches are being viewed in the context of two broad categories: site-based approaches and clade-based approaches (Borregaard *et al.*, 2014). Site-based approaches use null-model sampling of a regional species pool to develop an expected pattern of phylogenetic relatedness, assuming a group of species is drawn from the

regional pool irrespective of their ecologies. If the observed pattern of phylogenetic relatedness of the species in an assemblage (i.e. groups of co-occurring species that may or may not be interacting ecologically) deviates from the null expectation, this pattern is then interpreted as the outcome of underlying ecological processes (e.g. competition or abiotic filtering; Lovette & Hochachka, 2006; Slingsby & Verboom, 2006; Helmus *et al.*, 2007; Gomez *et al.*, 2010). Clade-based metrics examine relationships between sister clades, and have traditionally focused more on questions related to evolutionary history, like inferring the relative importance of different modes of speciation based on degree of range overlap (Barraclough & Vogler, 2000). Recently, arguments have been made for the necessity of integrating these two alternative approaches in order to disentangle the influences of evolutionary history and ecological processes on biotic assembly (Wiens, 2012; Warren *et al.*, 2014).

Efforts to combine site-based and clade-based approaches have examined shifts in patterns of relatedness at different phylogenetic scales (Borregaard *et al.*, 2014) and incorporated general patterns expected to result from speciation into null expectations (Pigot & Etienne, 2015). These advances, while significant, focus on developing regional species pools instead of reconstructing evolutionary histories. However, evolutionary history is complex and processes like allopatric speciation can result in both general and lineage-specific patterns of phylogenetic relatedness, even at small spatial scales.

The extent to which evolutionary history has resulted in non-random phylogenetic structure in contemporary assemblages is an empirical question. To assess the degree to which current research may be erroneously interpreting historical influence as an outcome of ecological processes, the effects of historical contingency must be distinguished from the effects of ecological processes on the species composition of assemblages (Wiens, 2012; Warren *et al.*, 2014). Attempts to apply an historical perspective to understanding assembly have relied on integrating phylogenetic data into studies of biotic assembly. Understanding phylogenetic relationships is necessary when developing expectations of co-occurrence as a result of evolutionary history, but it is not sufficient. To date, what has been missing is the development of historically driven expectations of co-occurrence, especially those derived from the mechanistic link between speciation and Earth history, and then the testing of those expectations using phylogenetic and biogeographical analyses.

By considering phylogenetic relationships in conjunction with historical biogeography (i.e. the relationship between Earth history, evolutionary processes, and species distributions; Lomolino *et al.*, 2010), one can reconstruct the accumulation of diversity in an area through space and time. A theoretical framework for incorporating evolutionary processes into studies of assembly is a prerequisite for examining the extent to which evolutionary history is driving the patterns being revealed by community phylogenetic research.

We propose a conceptual framework for the explicit incorporation of first-order processes of biotic diversification

(allopatry, speciation, and dispersion of biotas following the breakdown of barriers) into studies of assembly. This new approach, historical assembly analysis (HAA), develops an 'historical null expectation' for a local assemblage: the species composition that would be expected based solely on the evolutionary history of the lineages of species in the assemblage. HAA is based on historical biogeography of individual clades at the species level, and aims to reconstruct the assembly process across a dynamic spatial and biological landscape. This approach does not rely on generating 'null' expectations of occurrence based on resampling from a single species pool for all species in a local assemblage. Instead, HAA uses congruence and discontinuity in individual lineage histories within an assemblage, in conjunction with Earth history, to develop historical expectations for the presence/absence of individual species in an area. Below, we discuss how community phylogenetic approaches can be integrated with methods of historical biogeography and diversification analysis so that patterns resulting from evolutionary history can be distinguished from those produced by ecological processes.

THE ROLE OF EVOLUTION AND BIOGEOGRAPHY IN BIOTIC ASSEMBLY

Two empirical observations about organismal distributions provide insight into biotic assembly. First, the large majority of species are not widespread but are restricted in distribution; they are endemic to an area of some spatial extent. This results in differences in taxonomic composition across areas (Buffon's law; Nelson, 1978). Second, biotas have historical structure: groups of species sharing a recent common ancestor (clades) are non-randomly distributed (Lynch, 1989). Congruent patterns of phylogenetic relatedness across space-time have been repeatedly identified in independent phylogenetic lineages (Nelson & Platnick, 1981; Morrone, 2014). Moreover, we have increasingly understood the influence of geological and climatic history on the distribution of taxa at all taxonomic levels as well as across broad temporal and spatial ranges (Rosen, 1978; Riddle *et al.*, 2008).

Whenever allopatric speciation generates new diversity, it produces consistent spatial patterns of relatedness (Warren *et al.*, 2014; Pigot & Etienne, 2015). For example, as vicariant barriers arise and induce speciation, the resulting sister species do not co-occur; rather, they are isolated from each other by the barrier that caused speciation (Fig. 1). In the absence of this historical knowledge, if a study area were situated on one side of a barrier that resulted in speciation, the apparent pattern – phylogenetic overdispersion, or non-overlapping ranges of closely related species – might be interpreted as evidence of competitive exclusion instead of allopatric speciation (Fig. 1). Because the origin of a barrier can induce speciation across multiple lineages within an assemblage, single vicariant events often result in congruent distributional patterns of phylogenetic relatedness among allopatric sister species, or across entire biotas (Nelson & Platnick, 1981; Riddle *et al.*, 2008; Morrone, 2014). Consequently, vicariant speciation

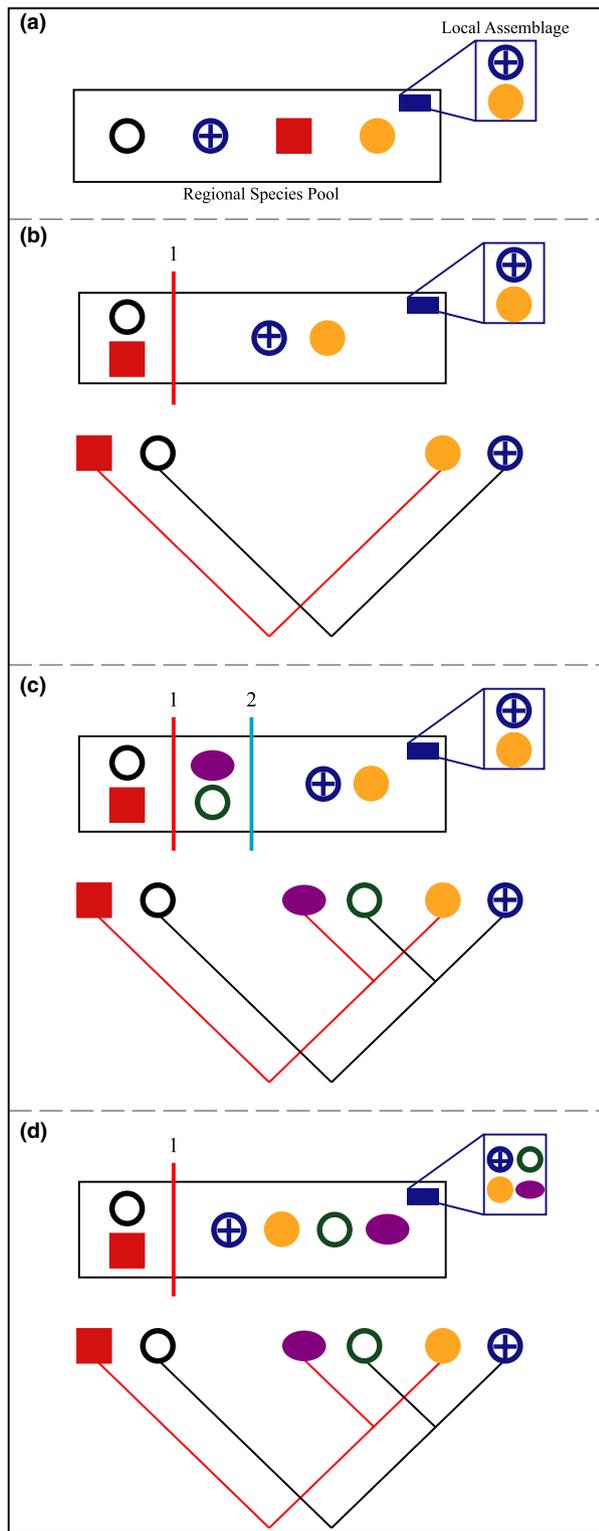


Figure 1 Biotic assemblages are structured by evolutionary history. (a) Nonhistorical approaches to assembly analysis typically view assemblages of species as a subsample of a ‘regional species pool’, with local composition interpreted as the result of ecological processes. (b–d) An historical approach, in contrast, may discover that local species composition is evolutionarily contingent. (b) Landscapes are dynamic, and if a vicariant barrier (line 1) divides a region, it can induce congruent patterns of speciation in some species, resulting in sister species distributed in separate historical areas and phylogenetically overdispersed patterns. (c) If the region is further divided by a second vicariant event (line 2), the historical signature is stronger because now there is three-taxon and three-area congruence. (d) If a barrier breaks down (e.g., barrier 2), secondary sympatry can occur, resulting in phylogenetic-clustering locally. Allopatry, speciation, and dispersion after barriers decay create complex patterns as historical events are layered on top of one another.

Emerging patterns in the phylogenetic structure of assemblages, like a shift from phylogenetic overdispersion to clustering as the spatial extent of the analysis increases, have traditionally been attributed to different ecological assembly rules operating at different spatial scales, or extent (Slingsby & Verboom, 2006; Swenson *et al.*, 2006; Cavendar-Bares *et al.*, 2009; Vamوسي *et al.*, 2009; Emerson *et al.*, 2011), but those patterns likely reflect a significant influence of history. As the size of the area of analysis changes, the relationship between the study area and historical area(s) can change, potentially changing the expected pattern of phylogenetic relatedness from overdispersion to clustering, especially when the study area spans across multiple speciation barriers. For example, in Amazonian birds, river formation is often invoked as the mechanism by which speciation occurs. In this system, therefore, as the study area increases in size and crosses the boundaries of historical areas (i.e. the study area spans two sides of a river that induced speciation upon its formation), species with different historical areas will be found in the study area, and those species will likely be closely related due to the spatial outcomes of speciation (i.e. sister species are likely to be present in adjacent areas of endemism).

While the spatial outcomes of evolutionary history may appear simple, they grow increasingly complex as areas are further subdivided by barriers, some species fail to speciate, and barriers break down leading to secondary sympatry. The problem is more acute when the ‘species pool’ includes species with incongruent historical areas (e.g. species from two areas of endemism) or when many, or most, species present in a study area dispersed across a physical or ecological barrier to reach the area (Cooper *et al.*, 2008; Emerson & Gillespie, 2008; Cardillo, 2011). The variety of processes that are constantly acting in concert, and the potential for different outcomes for different species with shared spatial histories, challenge the notion that the complexity of the evolutionary patterns in the assembly of a biota can be captured without reconstructing lineage-specific histories. Even if one accepts that a species pool is not static over time (Cavendar-Bares *et al.*, 2009; Pigot & Etienne, 2015), the concept itself con-

necessarily results in patterns of phylogenetic overdispersion. Within a single clade, vicariance produces what we will call *historical areas*: areas that are delineated by barriers that led to isolation and speciation, and the area is the initial range of a species at the time of speciation. When multiple species have congruent historical areas, those areas constitute an area of endemism (Fig. 2).

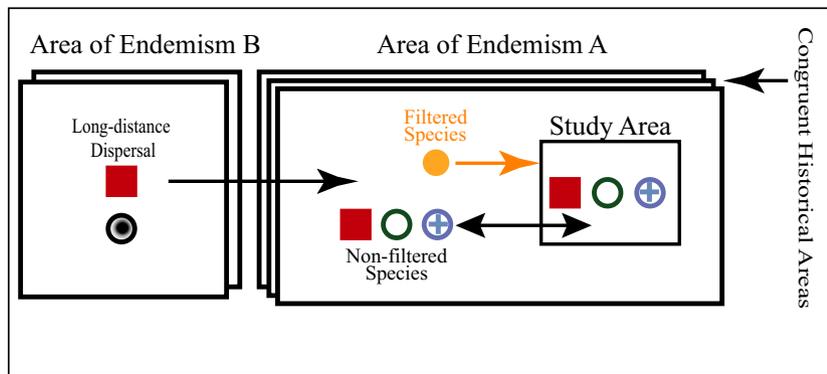


Figure 2 Conceptual diagram of historical biotic assembly. A study usually begins with the choice of an area ('Study Area') and group of organisms ('Target Species') to study. Historical analysis depends on understanding the historical area for each target species. The size of these areas is typically constrained by the barriers that induced speciation, which may be different across species even within a given taxon (e.g. birds). However, historical areas are often congruent across multiple taxa, resulting in an area of endemism. Assemblages are outcomes of allopatry, speciation, and dispersal, and must be reconstructed by identifying the historical areas for individual target species. Ecological processes may only be responsible for filtering species with historical areas that contain the study area.

strains thinking about how assemblages have been structured by evolutionary processes and raises the question, 'How was the pool itself assembled?'

By first considering species in assemblages to be the outcome of *in situ* diversification rather than filtered from an exogenous regional species pool, it becomes possible to incorporate the complexity of biogeographical history into traditional null expectations. Once the influences of allopatry, speciation and the dispersion of biotas on patterns of co-occurrence are explicitly reconstructed for individual species' lineages, one can search for deviations from these expected historical patterns (the 'historical null') and then identify ecological explanations for them.

HISTORICAL ASSEMBLY ANALYSIS

Phylogenies and geographical distributions provide the basic data for reconstructing the landscape features that are likely associated causally with particular speciation events, as well as with the history of connectivity of areas and their biotas (Donoghue & Moore, 2003; Riddle *et al.*, 2008; Ree & Sanmartín, 2009; Ribas *et al.*, 2012). The fields of systematics and historical biogeography have developed methods for interpreting these data, and can inform the integration of evolutionary processes into ecological studies of biotic assembly. Integration of Earth history, climate and historical patterns of diversification provide testable explanations for the variation in assemblage composition that can be attributed to evolutionary history alone.

We propose HAA, a conceptual framework for integrating evolutionary history into biotic assembly, in which phylogenetic and biogeographical tools are used to reconstruct the histories of lineages through time and space (Table 1). HAA focuses on discovering historical areas for each lineage in an assemblage, which is accomplished through an iterative process of testing biogeographical hypotheses. Generalities and

mechanistic processes can then be discovered by examining the relationships among the diversification histories of co-occurring lineages, on the one hand, and Earth history on the other (Crisp *et al.*, 2011).

When a group is chosen for assembly analysis, its constituent species and their potential biotic interactions can be seen as a consequence of the history of the area as well as species-specific evolutionary dynamics. Area histories are fluid, with changes in landscape and species composition themselves potentially changing ecological interactions. Thus, ecological interactions operate within a dynamic historical context to influence the structure of one or more assemblages within the study area.

The goal of HAA is to partition the causal dynamics of species composition within an assemblage into factors that are a consequence of species evolutionary histories and the factors that are a function of local ecological dynamics. Although the precise methods to develop an historical null expectation will vary across studies, there are conceptual steps that can be followed in undertaking HAA in any system amenable to phylogenetic and historical biogeographical analyses (Table 1). The first step to HAA is to delimit the study area that is relevant for the species of interest. The study area could be as spatially restricted as a single study plot, or as large, for example, as an area of endemism or a biome (such as Amazonia). The size of the study area will likely be related to the species being studied ('target species'). Although Amazonia may be too large and complex to study the assembly of its butterfly fauna – with its high diversity and many small areas of endemism – it might be a reasonable study area for analysis of birds or mammals. If the study area were a local assemblage (i.e. of limited spatial extent), a broader choice of study taxa could be possible. This step in HAA establishes the context for all subsequent steps and entails delimiting the boundaries of an assemblage and quantifying its diversity (Magurran & McGill, 2011; Morin, 2011).

Table 1 Using historical assembly analysis (HAA): proposed steps to understand the influences of evolutionary history on species assembly across spatial and temporal scales.

Protocol	Objectives	Methods and approaches	References
1. Delimit the area of interest ('study area') and identify the relevant species ('target species') within the assemblage	<ul style="list-style-type: none"> Set the spatial and taxonomic context for subsequent steps, linking HAA to the specific questions of the study and beginning to establish the spatial and temporal scales of the analysis 	<p>Use ecological and taxonomic background knowledge</p> <p>Employ biodiversity assessments and/or species inventories</p>	<p>Magurran & McGill (2011)</p> <p>Morin (2011)</p>
2a. Understand the general hierarchical-historical and spatial context of the study area and the target species	<ul style="list-style-type: none"> Identify the spatial extent of distributions for the target taxa and their potential close relatives 	<p>Map distributions of target species and close relatives. Identify patterns of distributional congruence (areas of endemism). When relevant use distributional modelling</p>	<p>Arias <i>et al.</i> (2011)</p> <p>Cracraft (1985)</p> <p>Goloboff (2007)</p> <p>Kreft & Jetz (2010)</p>
2b. Reconstruct the phylogenetic history of the target species in the assemblage and their close relatives (as determined in 2a), and estimate the timing of their clade's diversification	<ul style="list-style-type: none"> Provide an historical hypothesis for all relevant taxa and estimate their timetree Identify the original ranges of species, thus identifying likely historical areas for each target taxon's lineage 	<p>Conduct a phylogenetic analysis using parsimony, likelihood, or other model-based methods</p> <p>Construct a fossil calibrated timetree using Bayesian or likelihood methods</p>	<p>Arbogast <i>et al.</i> (2002)</p> <p>Drummond <i>et al.</i> (2012)</p> <p>Felsenstein (2004)</p> <p>Swofford <i>et al.</i> (1996)</p> <p>Yang & Rannala (2006)</p>
2c. Reconstruct the biogeographical history across clades	<ul style="list-style-type: none"> Understand the area relationships for the target species and their relatives Identify potential barriers responsible for allopatry Reconstruct the history of vicariance, dispersal, and extinction 	<p>Carry out a biogeographical area analysis, testing hypothesized histories</p> <p>Conduct an ancestral-area reconstruction</p>	<p>Nelson & Platnick (1981)</p> <p>Crisp <i>et al.</i> (2011)</p> <p>Hovenkamp (2001)</p> <p>Porzecanski & Cracraft (2005)</p> <p>Ree & Smith (2007)</p> <p>Ronquist & Sanmartín (2011)</p>
3. Reconstruct environmental change within and across all relevant historical areas	<ul style="list-style-type: none"> Identify and describe changes in Earth history (geomorphology, sedimentary, climatic, palynological, etc.) relevant to the biotic history of the assemblage Identify physical factors that have influenced the landscape within which the assemblage is embedded Integrate data on distributional patterns to identify barriers, their timing, and their potential loss 	<p>Perform tectonic, palaeohydrology, and geomorphological analyses</p> <p>Examine palaeontological and palynological studies</p> <p>Leverage remotely sensed data to understand potential changes in the landscape (e.g. Shuttle Radar Topography Mission data)</p> <p>Conduct palaeoclimate modelling</p>	<p>Badgley <i>et al.</i> (2008)</p> <p>Cheng <i>et al.</i> (2013)</p> <p>Campbell <i>et al.</i> (2006)</p> <p>Picard <i>et al.</i> (2008)</p>
4. Synthesize across steps 2–3	<ul style="list-style-type: none"> Partition causation for co-occurrences into historical and ecological factors Reconcile the history of biotic assembly and Earth history 	<p>Match the temporal patterns of biotic and Earth history and establish causal explanations for linkages</p>	<p>Moen <i>et al.</i> (2009)</p> <p>Picard <i>et al.</i> (2008)</p> <p>Ribas <i>et al.</i> (2012)</p> <p>Wiens (2011)</p>

Once a study area has been delineated, the second step is reconstructing the history of the assemblage in that area, which requires placing the study area into a broader spatial context, defined by the histories of speciation of the species being analysed (Fig. 2). In order to do this, one identifies the distributions and original ranges of members of the assemblage and their close relatives to identify the barriers potentially responsible for speciation. Understanding the historical context of the study area is an iterative process; general patterns, like areas of endemism, may guide initial

taxonomic sampling for more detailed phylogenetic and historical biogeographical analyses that provide lineage-specific histories, allowing the relevant historical areas to be discovered for each target species (Table 1, Steps 2a–2c).

By identifying patterns of congruence in the distributions of target species and their close relatives (e.g. if the distributions of target species and their close relatives largely follow the boundaries of areas of endemism; Cracraft, 1985; Goloboff, 2007; Kreft & Jetz, 2010; Arias *et al.*, 2011), one can understand the hierarchical structure of

distributions. For example, a species may be endemic to a single area of endemism, its genus may be endemic to a region, and the family may be endemic to a continent (Table 1, Step 2a). Historical areas can be of variable size depending on the historical barriers that led to isolation and speciation of the target species within that area. The size of historical areas can be different for different species within the same taxonomic groups (e.g. multiple species of birds within the same genus), or be consistent due to conserved dispersal abilities. Thus, reconstructing patterns of speciation using phylogenetic and biogeographical analysis to understand lineage-specific histories is key to deciphering the causal dynamics of co-occurrences, and to identifying the relevant historical area for each target species. Central to developing a detailed understanding of historical areas is the iterative process of identifying the relevant close relatives of the target species, reconstructing their phylogenetic relationships, and then assessing their spatial history using methods of historical biogeography (Table 1, Steps 2b-2c).

Time-calibrated phylogenies reveal both evolutionary relationships and timing of diversification for the target species and their close relatives (Swofford *et al.*, 1996; Arbogast *et al.*, 2002; Rannala & Yang, 2003; Felsenstein, 2004; Drummond *et al.*, 2012). Phylogenies also enable the delineation of historical areas and the use of historical biogeography to discover shared historical relationships across lineages and areas (Nelson & Platnick, 1981; Hovenkamp, 2001; Porzecanski & Cracraft, 2005; Ree & Smith, 2007; Ronquist & Sanmartín, 2011). For example, multiple species in the Inambari area of endemism in south-western Amazonia are sister to species distributed in adjacent areas of endemism in southern or north-western Amazonia (Ron, 2000; Ribas *et al.*, 2012); therefore, it is necessary to incorporate those other biogeographical regions into the analysis. If phylogenies are time-calibrated, speciation events can potentially be associated with the events in Earth history that established allopatry and speciation (Crisp *et al.*, 2011; Ribas *et al.*, 2012). This may reveal a persistent role for these barriers in limiting range expansion via dispersion across the landscape, and can potentially explain the absence of certain species from an assemblage. Long-distance dispersal events can also be inferred using phylogenies and geographical distributions through the discovery of target species that do not share biogeographical or temporally congruent patterns with other members of the assemblage (Crisp *et al.*, 2011; Ronquist & Sanmartín, 2011). Through historical biogeographical analysis one can reconstruct area-relationships (i.e. the history of geological connectivity among areas) and potentially identify species that may be absent from an area due to biogeographical history alone.

The third step of HAA is to identify the potential changes in Earth history (e.g. geomorphological changes, climatic changes, etc.) that may have shaped biotic distributions (Table 1, Step 3). Patterns of speciation and biogeography

across groups can be used in connection with reconstructions of landscape change to understand how physical factors have shaped those landscapes and their constituent species during assembly (Campbell *et al.*, 2006; Badgley *et al.*, 2008; Picard *et al.*, 2008; Cheng *et al.*, 2013).

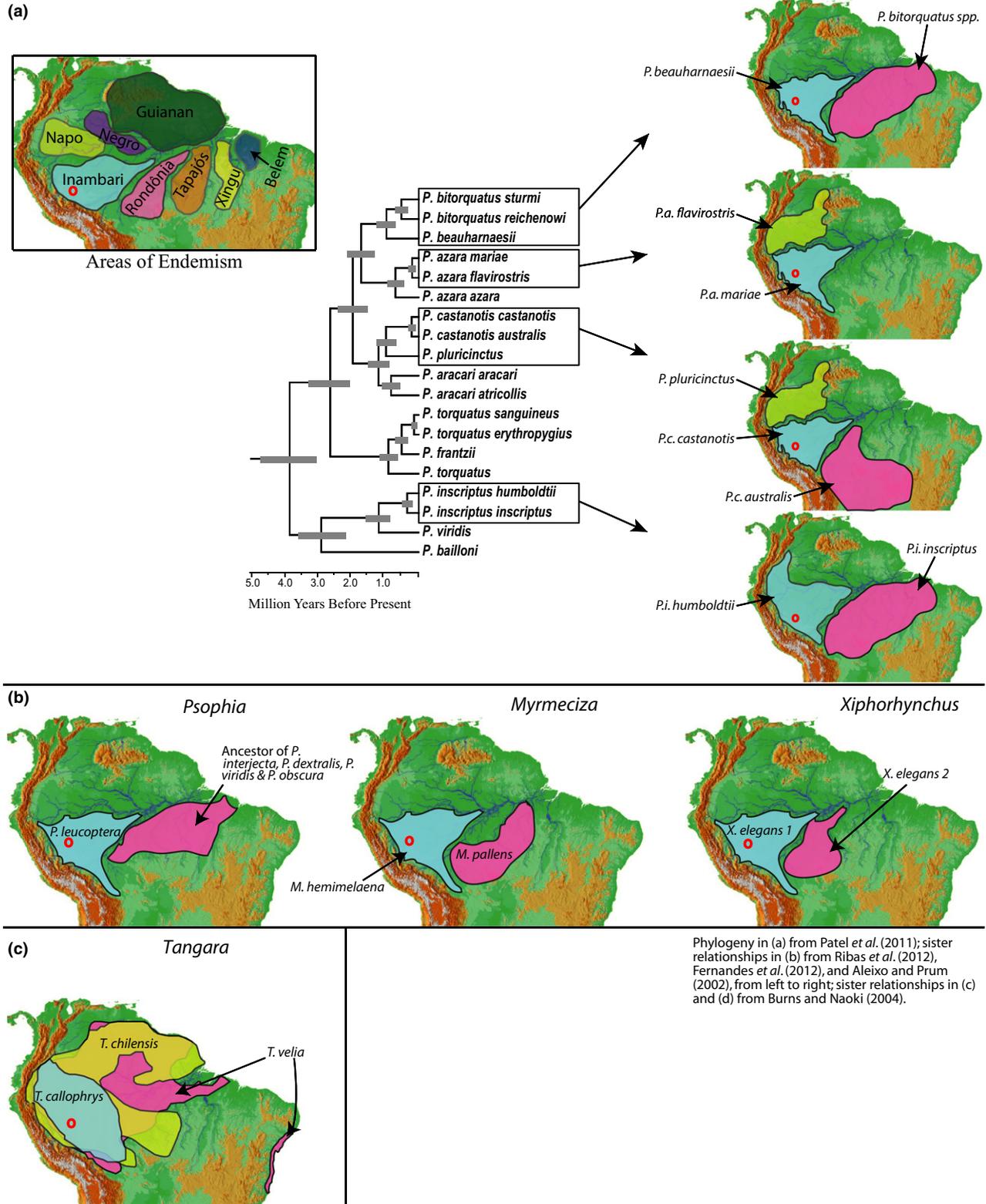
The final step of HAA is to synthesize across all previous steps, matching the timing and spatial patterns of biotic diversification with Earth history in order to understand the causal linkages between the two. This step establishes an historical expectation of co-occurrence in a local assemblage. Contemporary barriers such as rivers that led to speciation can be expected to limit co-occurrence of the resulting sister species or sister clades. Past barriers responsible for ancient speciation events (e.g. tectonic processes in the Andes, former connections of Amazonia and the Atlantic Coast Forest, or palaeoriver drainages) may have since disappeared, allowing for secondary sympatry of sister lineages in a local assemblage. This process of allopatry of populations, speciation and the breakdown of barriers allowing for secondary sympatry has led to the accumulation of diversity in local assemblages. By reconstructing these processes through time for an area and the biota found there, one can view the composition and landscape dynamics of local assemblages through time and identify persistent barriers of evolutionary significance that continue to shape species composition in an area. Once expectations of assemblage composition based on HAA have been developed, deviations from those expectations can be attributed to ecological processes. For example, if there is evidence that a barrier that induced speciation across a number of lineages has since broken down, but two of the sister species remain allopatric, this may be evidence of ecological interactions limiting co-occurrence. To demonstrate how HAA might be applied to a group to reconstruct biotic assembly, we apply HAA to a group of birds at an iconic biological research station in South America.

THE ASSEMBLY OF *PTEROGLOSSUS* TOUCANS AT COCHA CASHU: AN EMPIRICAL EXAMPLE OF HAA

Four species of *Pteroglossus* toucans are found at the 97 ha Cocha Cashu Biological Station; they will serve as an exemplar assemblage of interest, providing an empirical example of how to conduct HAA. The analysis could be expanded to include more species, for example all fruit-eating birds, but the methodological steps discussed here would not change. Defining the assemblage of interest, the first step of HAA, is question-driven. For example, we may want to know why and how the four species of *Pteroglossus* came to co-exist and what role competitive exclusion may have played in limiting the co-occurrence of other *Pteroglossus* at Cocha Cashu (Table 1). To begin, we want to understand the historical and spatial context of the *Pteroglossus* assemblage (Table 1, Step 2a). Their distributions, and those of their close relatives (Fig. 3), reveal a spatial context in which Cocha Cashu is in

the Inambari area of endemism, which is nested in Amazonia, and finally nested in South America. This spatial hierarchy is confirmed by a comparison to the congruent distributions of additional bird taxa (Fig. 3b). The assemblage can then be studied in relation to evolutionarily relevant historical areas

and barriers (Table 1, Step 2a). Birds at Cocha Cashu usually have their closest relatives in other parts of Amazonia, but species found in the Atlantic Forest, the Choco west of the Andes, or in Central America could conceivably also be sister to the Amazonian species. This prioritizes Amazonian species



for sampling in the phylogenetic reconstruction of the group, but also highlights the fact that sampling more broadly to include other South and Central American *Pteroglossus* species could potentially be informative (Table 1, Step 2b). Phylogenetic analysis of *Pteroglossus* identifies the sister taxa of the four target taxa and provides information about the timing of the diversification of the clade (Fig. 3a).

We can use the phylogenetic relationships and timing of diversification recovered by Patel *et al.* (2011) as a framework for understanding the relevant area-relationships (Table 1, Step 2c) as well as potential historical explanations for the group's diversification (Table 1, Step 3). The divergence and distributions outside of Amazonia of the *P. torquatus* group (found west of the Andes and in Central America) and *P. bailloni* (present in the Atlantic forest) are evidence of deep historical structure within the genus in South America. Within Amazonia all *Pteroglossus* taxa are isolated from their closest relative(s) by a major river. All four *Pteroglossus* taxa at Cocha Cashu have sister taxa that are allopatric and isolated from their sister taxon by either the Solimões or Madeira Rivers. This implies that such barriers, once formed, place important constraints on dispersion, which influences the assembly process in terms of its temporal pattern and taxonomic composition. This spatial pattern, taken in conjunction with similar patterns for other Amazonian groups (e.g. *Psophia*, *Myrmeciza* and *Xiphorhynchus*; Fig. 3b), suggests that these barriers are likely causally associated with the area of endemism (Inambari) that contains Cocha Cashu.

Incorporating the timing of diversification of this group we can synthesize and understand the assembly of the target taxa in relation to landscape change (Table 1, Steps 3 and 4). The assembly of *Pteroglossus* at Cocha Cashu was not a simultaneous process. Although the time-calibrated phylogeny (Patel *et al.*, 2011; Fig. 3a) identifies spatial congruence in three taxa having sister groups across the Madeira river, they differ temporally. Thus, *P. inscriptus humboldtii* and *P. castanotis castanotis* have sister taxa resulting from speciation at roughly 400 ka, whereas *P. beauharnaesii* diverged from its sister species c. 1.5 Ma. This suggests that *P. beauharnaesii* was present at Cocha Cashu prior to *P. inscriptus humboldtii* and *P. castanotis castanotis*, both of which originated at approximately the same time. These spatio-temporal patterns also character-

ize other groups. For example, *Psophia leucoptera* is found at Cocha Cashu and diverged from its sister group, which is also distributed east of the Madeira River, c. 1.7–1.8 Ma (Ribas *et al.*, 2012). *Pteroglossus azara mariae* shows a different spatial pattern, with its sister taxon north of the Solimões River, but it too diverged c. 400 ka.

Two hypotheses can explain temporal disparity in the assembly of *Pteroglossus* at Cocha Cashu. One is dispersal across the Madeira c. 1.0–1.5 Ma and then later c. 400 ka. However, a more likely hypothesis that accounts for congruent biogeographical patterns is that of river history. River barriers can wax and wane, but they also meander and are involved in river capture events. We hypothesize that there were one or more instances of 'mega-river capture' involving the Madeira that transferred some of the biota from one side to the other. Importantly, there is evidence within Amazonia of major river capture as well as rapid shifts in directionality (Almeida-Filho & Miranda, 2007; Rossetti & Valeriano, 2007), including for the Madeira (Hayakawa & Rossetti, 2015).

Conclusions about the assembly of *Pteroglossus* at Cocha Cashu based on HAA are different from those based on a traditional community phylogenetic approach. For this analysis, we again considered the four *Pteroglossus* species found at Cocha Cashu to be the local assemblage. We compared the mean nearest-taxon distance (MNTD) of the species in the local assemblage to the expected MNTD based on null sampling from a regional species pool. We implemented this traditional community phylogenetic approach using the PHYLLOCOM software (Fig. 4; Webb *et al.*, 2008). When applying either of two conceptions of a regional species pool, the entire genus or only those *Pteroglossus* found east of the Andes, Cocha Cashu appears to show phylogenetic overdispersion (Fig. 4). Although not significant – likely due to the small number of taxa included for simplicity – this example demonstrates three key points. First, allopatry of close relatives is expected and can result in signals of phylogenetic overdispersion; this is in agreement with Pigot & Etienne (2015). Second, as larger regional species pools are used, the phylogenetic signal can be expected to shift towards phylogenetic clustering, as more distantly distributed species are typically more distantly related, reflecting the hierarchical nature of area-relationships. Third, as the size of the assemblage is

Figure 3 The imprint of history on an assemblage. The Cocha Cashu research station (red circle) is located within the Amazonian Inambari area of endemism. (a) Four species of *Pteroglossus* toucans co-occur there: *P. inscriptus*, *P. mariae*, *P. castanotis* and *P. beauharnaesii* (Terborgh *et al.*, 1990). Sister taxa of these species are not found at Cocha Cashu, a pattern that might be interpreted as evidence of competitive exclusion. Yet, allopatry is expected based on the congruent speciation histories within *Pteroglossus*. For taxa endemic to the Inambari area, the Rio Madeira (separating the Inambari and Rondônia areas) and the Rio Solimões (separating the Inambari and Napo areas) are commonly associated with allopatric distributions for many of the sister taxa of species at Cocha Cashu, including *Pteroglossus*. (b) These highly congruent patterns also exist in other taxonomic groups, such as trumpeters (*Psophia*), antwrens (*Myrmeciza*) and woodcreepers (*Xiphorhynchus*). While congruent patterns of relatedness are common, these patterns can be obscured by the failure of some taxa to speciate, long-distance dispersal, a dynamic landscape that can generate complex patterns even within groups, and importantly, the application of different taxonomic practices. (c) For example, *Tangara chillensis* and its pair of sister taxa (*T. callophrys* and *T. velia*) are all found at Cocha Cashu. Thus, phylogenetic history is present within Amazonia and should be taken into account when reconstructing assembly processes. Taken together, these examples show a pervasive and largely congruent imprint of speciation history on the distribution of taxa, and also demonstrate the danger of capturing the complexity of diversification histories in a single 'species pool'.

increased, encompassing multiple historical areas, there is a clear shift from phylogenetic overdispersion to phylogenetic clustering. All of these outcomes are consistent with predictions that can be made if evolutionary history is producing spatially nested patterns of phylogenetic relatedness.

Historical assembly analysis provides an expectation of co-occurrence that can serve as an historical ‘null’ hypothesis in community phylogenetic analyses. For example, because all four *Pteroglossus* species found within Inambari are also found at Cocha Cashu, the species composition of our assemblage seems to have been dictated entirely by evolutionary history. Neither biotic interactions nor abiotic filtering prevented the *Pteroglossus* species not found at Cocha Cashu from coexisting with the target taxa; rather, the other *Pteroglossus* are absent from the assemblage because of historical reasons. If other sites within Inambari were surveyed, and one or more of the target taxa were missing, those absences might be attributable to ecological processes operating at a local level, although neutral processes such as demographic stochasticity should be ruled out first (Hubbell, 2001). While these exemplar taxa had congruent historical areas, this may not always be the case, even for close relatives (e.g. *Tangara* at Cocha Cashu; Fig. 3c), highlighting the necessity of HAA’s lineage-based approach to reconstructing assembly. Thus, only after historical expectations have been formulated through HAA can methods for identifying the influence of ecological processes (e.g. Maurer *et al.*, 2013; Price *et al.*, 2014) be applied. By providing insights into the timing and order of the accumulation of diversity, HAA may facilitate the expansion of existing studies of the importance of these aspects of assembly on contemporary ecology (e.g. Leopold *et al.*, 2015).

HISTORICAL ASSEMBLY ANALYSIS OF TRAIT EVOLUTION

In addition to understanding the species composition of assemblages, HAA provides a powerful historical context within which ecological processes relevant to biotic assembly can be examined. For example, the role of traits in biotic assembly is a long-standing area of interest for many ecologists. Most ecological characteristics that can influence the assembly process, such as trophic guild membership and functional traits, typically reflect heritable components of the phenotype; hence, they can be influenced by evolutionary history. As such, they are amenable to historical analysis, including ancestral-state reconstructions and modelling of trait evolutionary dynamics using methods in comparative phylogenetics to model trait evolution and to characterize niche conservatism (Schluter *et al.*, 1997; Losos *et al.*, 1998; Pagel, 1999; O’Meara *et al.*, 2006; Moen *et al.*, 2009; Mayfield & Levine, 2010).

Reconstructing the evolution of a trait along a phylogeny makes it possible to estimate the points at which that trait changed states. Based on the historical biogeographical and environmental reconstructions used in HAA to understand co-occurrence, one can determine the biological context within which those trait-state changes occurred. For example,

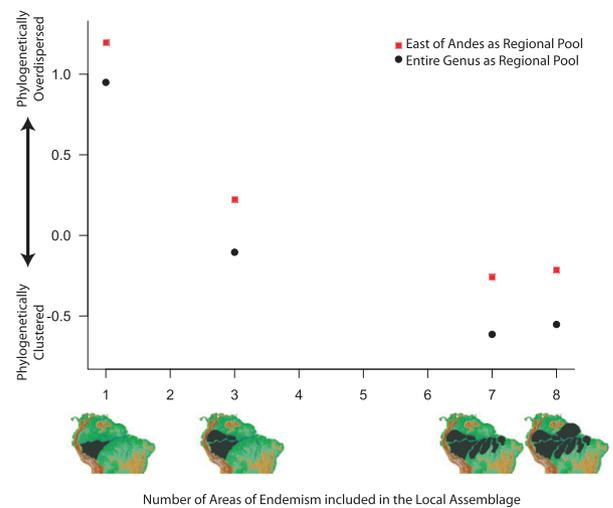
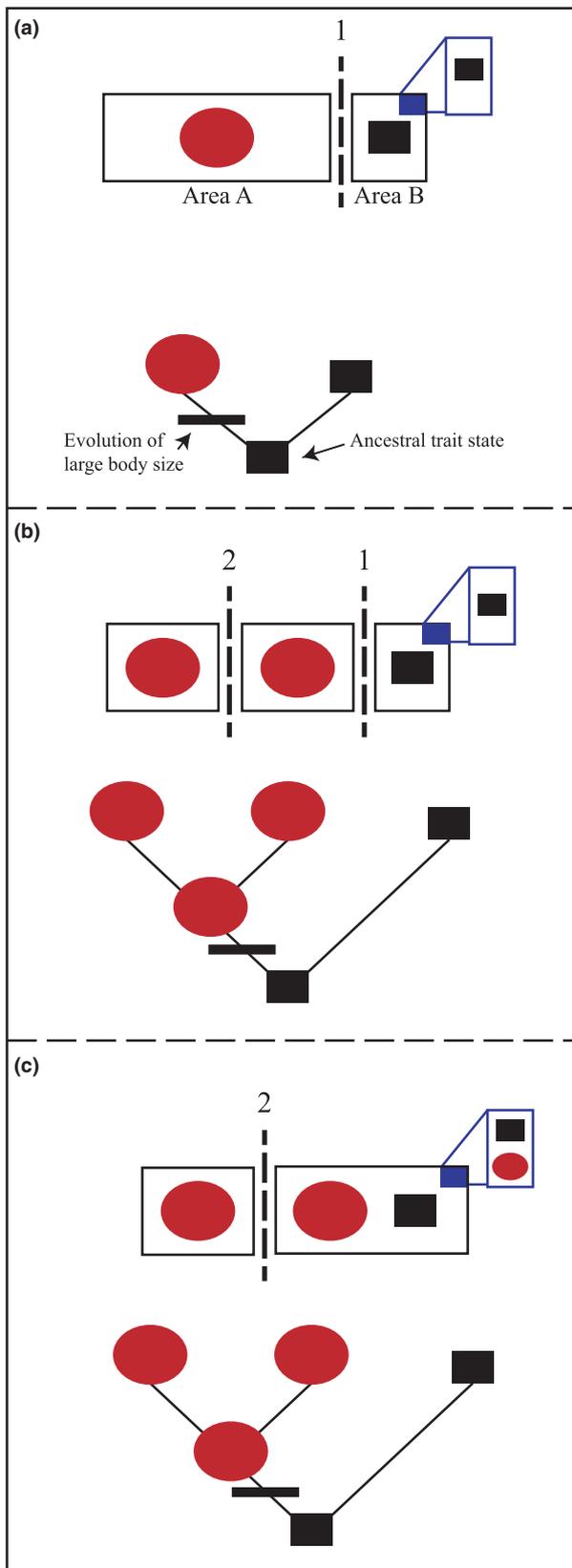


Figure 4 Community phylogenetic analysis of the assembly of *Pteroglossus* sp. of Amazonia across scales and species pools. Phylogenetic clustering versus overdispersion is measured as: [observed mean nearest-taxon distance (MNTD) of an assemblage – the MNTD for randomly selected taxa from the regional species pool]/standard deviation of MNTD of randomly selected taxa, and calculated using PHYLOCOM. Positive values indicate that the MNTD of the species in an assemblage is greater than expected by chance (i.e. the species are less-closely related than expected by chance; phylogenetic overdispersion), while negative values indicate the MNTD of species in an assemblage is less than expected by chance (i.e. the species are phylogenetically clustered). When all species in *Pteroglossus* are included in the regional species pool (black points), all assemblages appear to be more clustered than if only the *Pteroglossus* east of the Andes are included in the regional species pool (red points). Additionally, if the local assemblage is expanded from the *Pteroglossus* found at Cocha Cashu (the first point), to the *Pteroglossus* species found in areas west of the Rio Madeira and Rio Negro (second point), or areas west of the Rio Madeira and south of the Amazon River (third point), or even all of Amazonia (fourth point), the local assemblage begins to encompass multiple areas of endemism. As the local assemblage increases in size in relation to the regional species pool, there is a clear shift from phylogenetic overdispersion towards clustering, as would be expected if speciation were driving patterns of relatedness across the landscape. This pattern is sensitive to the order that areas are added, but there is a consistent pattern towards phylogenetic clustering as the local assemblage is expanded in scope.

if two species that co-occur have different trait states (e.g. large and small bodies), HAA can provide the information necessary to determine whether that trait diverged before or after sympatry of the two species (Fig. 5). If either or both of the co-occurring species possesses a derived trait state (i.e. if an individual species’ trait diverged after secondary contact), it would then be appropriate to examine the potential eco-evolutionary drivers of that trait change in the biotic and environmental setting in which the species are sympatric. If, on the other hand, the trait states of the two species diverged prior to secondary sympatry, then there is no need to ascribe trait similarity or difference to biotic



interactions or environmental influences within that assemblage. As with the influence of history on expectations of co-occurrence, if spatially explicit phylogenetic analyses of trait

Figure 5 Historical assembly analysis provides essential context for understanding trait evolution. In this example, each shape represents a trait state: smaller black squares represent small body size and larger red ovals represent large body size. (a) In Area A, the species evolves a large body, whereas in Area B the ancestral small body size is retained. (b) If a vicariant event divides Area A (line 2), it is possible that both species will retain the ancestral state of ‘large-bodied’. (c) If the initial barrier (line 1) breaks down, the assemblage will have two closely related species, one with a large body and one with a small body. It would be inappropriate to consider biotic interactions (such as competition) between the two local species as a driver of trait divergence, as the different body sizes are the ancestral states of both species: the origin of large body size pre-dates sympatry of the large and small-bodied species.

evolution are not incorporated into studies of biotic assembly, patterns of trait convergence or divergence might be interpreted as outcomes of ecological interactions rather than historical contingency.

The *Pteroglossus* at Cocha Cashu provide an example of how one might take a historical approach to understanding trait evolution. Body sizes of co-occurring species could be interpreted as the outcome of character displacement that reduced interspecific competition (Schluter & McPhail, 1992; Grant & Grant, 2006). The genus *Pteroglossus* can be divided into large- and small-bodied taxa (based on weight data from Short & Horne, 2002). Using standard ancestral character estimation techniques (Schluter *et al.*, 1997), we reconstructed the evolution of body size (large- and small-bodied) onto the *Pteroglossus* phylogeny. Based on this reconstruction, we concluded that three *Pteroglossus* taxa at Cocha Cashu retained ancestral body sizes, the most recent transition having occurred roughly 2 Ma. This finding suggests that history can explain much of the variation in body size of the taxa at Cocha Cashu, and can serve to focus ecological study of this trait on the single taxon that has a derived trait state.

CHALLENGES TO CONDUCTING HISTORICAL ASSEMBLY ANALYSIS

Although conceptually simple, resolving patterns of co-speciation across clades requires extensive phylogenetic and distributional data, and faces some well-known challenges (Nelson & Platnick, 1981; Sanmartín & Ronquist, 2002), even assuming data are available and estimates of relationships are accurate. In some groups, a vicariant event may not lead to speciation, thus creating a widespread species in two or more areas. Long-distance dispersal can result in areas sharing species when those areas are not historically related, or dispersal can produce allopatry and speciation, in which case, the geographical pattern of sister species might not reflect the true historical connections among areas. In addition, species may be missing from areas due to extinction, even on relatively short time-scales (Oswald & Steadman, 2011), thus confounding area-relationships. Finally, barriers themselves are not necessarily stable over time and

can arise and disappear (Fig. 1), thus making the reconstruction of the history of area-relationships difficult based on extant species alone (Ronquist & Sanmartín, 2011). These factors combine to create complex relationships between areas and speciation events that can be specific to individual clades, necessitating reconstruction of biogeographical histories on a clade-by-clade basis (Bates *et al.*, 1998). Yet even in complex systems such as Amazonia, historical biogeographical analysis can recover congruent temporal and spatial patterns of speciation and diversification (Ron, 2000; Eberhard & Bermingham, 2005; Patel *et al.*, 2011). Integrating independent knowledge from geological or environmental history can add critical information for, or against, inferences about biotic history, highlighting the need for an interdisciplinary approach that involves specialists across disciplines who understand the biotic results and recognize the importance of trying to reconcile biotic and Earth history events (e.g. Ribas *et al.*, 2012).

CONCLUSIONS

The integration of community ecology, phylogenetics and biogeographical analysis has the potential to elucidate the mechanisms by which ecological assemblages are formed. HAA places assemblages within an historical context characterized by a history of allopatry, speciation and dispersion, as well as the explicit understanding that areas are dynamic, hierarchical and described by the joint evolutionary histories of their constituent species. We have endeavoured to outline a conceptual framework for using HAA to reconstruct biotic assembly in any system amenable to phylogenetic and historical biogeographical analyses (Table 1). Using historical approaches to frame the context of ecological processes will enable community phylogenetics to benefit from growing knowledge of phylogenetic history. This can facilitate the incorporation of time as well as the environmental and ecological background into assembly analysis. HAA also places assemblages in historical context, and would allow for comparative studies (e.g. Liu *et al.*, 2013; Troia & Gido, 2015) to be conducted at large extents and with explicit consideration of specific historical areas.

By applying an historical approach, the role of ecological interactions is circumscribed to their mechanistically proper scale, namely among individual organisms, not among species and higher taxa (Cracraft, 1989). Constraining the analyses of trait evolution to changes that occurred in the context of the assemblage being examined makes it possible to examine the influence of ecological interactions on those traits. As with co-occurrence, additional research is needed to quantify the importance of history for interpretations of trait evolution and, consequently, the role of traits in structuring assemblages.

Although HAA requires a significant amount of data, the rapid accumulation of detailed phylogenies for a wide array of taxa, as well as data about Earth history, are making it increasingly feasible to build historical models based on the processes that drive diversification and distributions. As phylogeneticists build trees at increasingly fine resolution and

with larger taxonomic sampling, the ability to examine the phylogenetic relationships of entire guilds or assemblages at the species-level is no longer a distant reality for some taxa (e.g. Tobias *et al.*, 2014), making HAA an increasingly powerful tool for studying assembly.

Taking an evolutionary approach to understanding assembly is important, not just because evolutionary processes have the potential to act at smaller spatial and temporal scales than previously appreciated (Hendry *et al.*, 2000), but primarily because current patterns of co-occurrence are the results of a history of speciation, dispersion of biotas, ecological interactions, and phenotypic evolution. Our call for an historical approach to examining assembly is intended to stimulate discussion regarding the incorporation of evolutionary processes in a more explicit way, and to urge restraint in interpreting results of community structure studies without controlling for the effects of history. This view also implies a need for collaboration across disciplines. No single discipline can be expected to bring the expertise needed to link Earth history and biotic history in order to understand patterns of co-existence and trait variation, and to understand how they might be relevant for the assembly process. How biotas have evolved and assembled into ecological communities across time and space is a complex problem, but a plethora of new methods, information and conceptual approaches make this an exciting time to study the assembly process, and suggest that many new insights are sure to come.

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BIOSKETCHES

Brian Weeks' research is focused on reconstructing the assembly of avian communities, particularly groups of Melanesian birds, and exploring the relationship between evolutionary history and community ecology.

Santiago Claramunt is interested in integrative phylogenetic and macroevolutionary approaches to unravelling the processes that generate biodiversity and its temporal and spatial patterns, mostly using Neotropical birds.

Joel Cracraft's research is focused on the systematics, evolution, and historical biogeography of birds.

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