

# A geography-aware reconciliation method to investigate diversification patterns in host/parasite interactions

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## Abstract

Cospeciation studies aim at investigating whether hosts and symbionts speciate simultaneously or whether the associations diversify through host shifts. This problem is often tackled through reconciliation analyses that map the symbiont phylogeny onto the host phylogeny by mixing different types of diversification events. These reconciliations can be difficult to interpret and are not always biologically realistic. Researchers have underlined that the biogeographic histories of both hosts and symbionts influence the probability of cospeciation and host switches, but up to now no reconciliation software integrates geographic data. We present a new functionality in the *Mowgli* software that bridges this gap. The user can provide geographic information on both the host and symbiont extant and ancestral taxa. Constraints in the reconciliation algorithm have been implemented to generate biologically realistic codiversification scenarios. We apply our method to the fig/wasp association and infer diversification scenarios that differ from reconciliations ignoring geographic information. In addition, we updated the reconciliation viewer *SylvX* to visualize ancestral character states on the phylogenetic trees and highlight parts of reconciliations that are geographically inconsistent when not accounting for geographic constraints. We suggest that the comparison of reconciliations obtained with and without such constraints can help solving ambiguities in the biogeographic histories of the partners. With the development of robust methods in historical biogeography, and the advent of next-generation sequencing that leads to better-resolved trees, a geography-aware reconciliation method represents a substantial advance that is likely to be useful to researchers studying the evolution of biotic interactions and biogeography.

## KEYWORDS

ancestral trait, biogeography, cophylogeny, host/parasite, reconciliation, software, tree visualization

## 1 | INTRODUCTION

Biotic interactions play a prominent role in species diversification. Interactions that result in long-term associations persisting over evolutionary timescales can sometimes lead to cospeciation, that is the concomitant occurrence of speciation in lineages that are ecologically associated (Brooks, 1981; Page, 1990, 1991). The idea that

such a pattern can occur first stemmed from parasitological studies suggesting that parasite classifications reflect the phylogenetic relationships of their hosts (Fahrenholz, 1913). Hafner and Nadler (1988) and Hafner et al. (1994) were the first authors to thoroughly test this assertion. They used the association between pocket gophers and their lice as a model system and provided a clear demonstration that the phylogenies of the two interacting lineages

were parallel. This study spurred further research on cospeciation. The developments of specific methods that aimed at testing the congruence of the phylogenetic histories of interacting organisms have since played an important role in the study of cospeciation. It is indeed these methods that moved cospeciation studies beyond visual comparisons of phylogenetic trees and ad hoc narratives for these visualizations. It soon became apparent that the study of the concordance between phylogenetic trees could be applied to reconciling gene trees and species trees (Page & Charleston, 1997, 1998), which further enhanced the interest of evolutionary biologists for methodological developments in this field.

Review articles (Brooks, Dowling, van Veller, & Hoberg, 2004; de Vienne et al., 2013; Doyon, Ranwez, Daubin, & Berry, 2011; Johnson & Clayton, 2004; Martínez-Aquino, 2016; Paterson & Banks, 2001; Stevens, 2004) all emphasize the diversity and the complexity of the scenarios that must be explored when testing for the congruence of speciation events in two interacting lineages. To compare host and parasite phylogenies, Brooks (1981) and Brooks and McLennan (1991) first developed a parsimony method (the Brooks Parsimony Analysis, BPA). In this method, the associations between hosts and their parasites are transformed into a matrix of host characters and the parsimony tree reconstructed from such a matrix is then compared to the host phylogeny. A decade later, Page and collaborators developed a fundamentally different method, called “tree reconciliation,” a term first coined in the work of Goodman, Czelusniak, Moore, Romero-Herrera, and Matsuda (1979) that compared gene and species trees. This method attempts to reconcile the phylogenetic history of the parasites with that of their hosts: the parasite phylogeny is “mapped” onto the host phylogeny (i.e., each node in the parasite tree is assigned to a node or a branch in the host phylogeny). In such a map, the diversification events of the parasites are linked to their host phylogenetic history and four types of events are considered: cospeciation events, host switches, sorting events and duplication events (Page, 1994a, 1994b) (see Methods for a description of each event). When graphically displayed, reconciliation maps greatly ease our understanding of the evolution of biotic interactions.

Algorithms to optimize reconciliations are numerous. One of the first reconciliation softwares, *TreeMap 2*, uses an algorithm called “Jungles” (Charleston, 1998) where each event is assigned a cost: the chosen reconciliations are the ones that have minimum costs. However, it generates in the process an exponential number of scenarios. Recent methods have proposed algorithms that are more efficient and can also just search for an optimal reconciliation: for example *Tarzan* (Merkle & Middendorf, 2005), *Jane* (Conow, Fielder, Ovadia, & Libeskind-Hadas, 2010), *Core-PA* (Merkle, Middendorf, & Wieseke, 2010), *Mowgli* (Doyon et al., 2010), *COALA* (Baudet et al., 2015), *ecceTERA* (Jacox, Chauve, Szollosi, Ponty, & Scornavacca, 2016), *Notung* (Stolzer et al., 2012), *EUCALYPT* (Donati, Baudet, Sinaimeri, Crescenzi, & Sagot, 2015) and *ILPEACE* (van Iersel, Scornavacca, & Kelk, 2014). In a phylogenomic context, the *ALE* (Szöllösi, Boussau, Abby, Tannier, & Daubin, 2012) and *ecceTERA* software accept a collection of bootstrap trees instead of a single tree to represent a gene family (parasites) evolution. By assembling subtrees from

different trees in this collection, they can build a gene (parasite) tree that best reconciles with the species (host) tree. Recently, the *RASCAL* software proposed the inference of suboptimal scenarios to reduce computing times (Drinkwater & Charleston, 2016). Cospeciation is witnessed on a reconciliation map whenever a node in the parasite phylogeny is mapped onto a node on the host phylogeny. Another requirement for demonstrating that two interacting lineages have cospeciated is to provide evidence of the temporal congruence of the cospeciation event in the host and parasite phylogenies (Page, 1991). Although reconciliation algorithms do not strictly enforce the simultaneity of cospeciation events, they can enforce time consistency in the sequence of evolutionary events, meaning that the parasite cannot switch back in time onto a host that no longer exists (i.e., a transfer cannot occur towards a node in the host phylogeny that has already split into child species at the time of the transfer event) (Merkle & Middendorf, 2005; Nøjgaard et al., 2017). This constraint is explicit in *Mowgli* (Doyon et al., 2010, 2011), *ecceTERA* (Jacox et al., 2016) and *RASCAL* (Drinkwater & Charleston, 2016). Hence, reconciliation methods have greatly improved in the last decade; algorithms are now efficient and some have solved the time consistency issue that affected some of the first methodological developments in the field. However, interpreting the scenarios that emerge from these inferences remains a difficult task. It is generally challenging to identify biologically realistic reconciliations. Much remains to be carried out to improve these inferences and translate them into evolutionary scenarios that give insights into the biological factors that govern the evolution of interspecific associations.

Some key information that can significantly improve our inferences but are overlooked in codiversification methods are the geographic locations of extant and ancestral nodes. Indeed, the biogeographic histories of interacting lineages necessarily constrain their common part of evolutionary history (Martínez-Aquino, Ceccarelli, Eguiarte, Vazquez-Dominguez, & de Leon, 2014; Nieberding, Jousset, & Desdés, 2010). Obviously, a cospeciation event can only happen between taxa that co-occur in the same area. The geographic context of both hosts and parasites also influences host switch events. In biotic interactions where the parasites can undergo long dispersal events, transfers can happen between allopatric hosts (i.e., hosts that do not live in the same geographic area). However, they are only possible if the geographic locations of the “sending host” (the host from which the switch is initiated) and the “receiving host” coincide with a dispersal event along the corresponding branch in the parasite phylogeny. Therefore, a more accurate mapping of cospeciation and host switch events can be obtained if the geographic locations of both hosts and parasites are known prior to conducting the reconciliation.

Methods for inferring historical biogeography from phylogenetic reconstructions have greatly improved in the last two decades. Early developments in historical biogeography aimed at reconstructing “area cladograms” that reflected the history of connections between areas of endemism for the group of organisms under study and used analytical tools that were very similar to the tools developed for the study of cospeciation using parsimony as the optimization criterion (e.g., BPA, see Morrone, 2009; for a review on cladistic biogeography and its

methodological developments). More recent probabilistic methods in the field of historical biogeography reconstruct ancestral geographic ranges on a dated phylogenetic tree on the basis of current species geographical distribution. They model the evolution of geographic areas on a phylogenetic tree using maximum-likelihood optimization or Bayesian inference, and incorporate divergence times into the inference process: the longer the phylogenetic branch, the higher the probability of geographic range shifts and the larger the uncertainty in the ancestral range estimates. Geographic areas can be treated as simple categorical characters that are reconstructed on the tree using, for instance, a stochastic Markov model of evolution. More biologically realistic and widely applied methods in historical biogeography, such as DEC (*Dispersal, Extinction, Cladogenesis*) (Ree, Moore, Webb, & Donoghue, 2005; Ree & Smith, 2008), model range evolution using different parameters for each biogeographic process (dispersal, range expansion or extinction). In addition to modelling these key processes, the main innovation of DEC is the incorporation of a time-dependent transition matrix that defines the transitions between geographic areas at different time intervals, to reflect how dispersal opportunities changed through time (e.g., changes in continental configuration) (see Ree & Sanmartin, 2009; Ronquist, Sanmartin, Futuyma, Shaffer, & Simberloff, 2011; for reviews on parametric biogeography). Fossil distribution and information on the climatic preferences of ancestral lineages can also be incorporated as constraints to improve biogeographic inference (Meseguer, Lobo, Ree, Beerling, & Sanmartin, 2015). Several conceptual and computational improvements have been implemented since the initial version of DEC (DEC + J, Matzke, 2014; DECC, Beeravolu Reddy & Condamine, 2016). Different biogeographic models have also been proposed (GeoSSE, Goldberg, Lancaster, & Ree, 2011; BayArea Landis, Matzke, Moore, & Huelsenbeck, 2013). As a result, robust biogeographic scenarios are now available for numerous lineages. Ancestral areas inferred by these methods can then serve as input for reconciliation analyses. In this study, we build on these advances to provide a geography-aware reconciliation method, pushing further the accuracy of scenarios proposed by such methods.

We first describe the constraints we enforce to ensure geographic consistency in reconciliations and how they were implemented in the *Mowgli* reconciliation software (Doyon et al., 2010). We also describe new options designed in the *SylvX* reconciliation viewer (Chevenet et al., 2016) to integrate and visualize annotations (e.g., geographic areas) of ancestral hosts and parasites, as well as to highlight zones that are geographically inconsistent. We then test these new developments on a mock data set and on a “textbook” example of cospeciation, namely the interaction between figs (*Ficus*) and their pollinating fig wasps (Cruaud et al., 2012; Rønsted et al., 2005; Wiebes, 1979).

## 2 | METHODS

### 2.1 | Extending *Mowgli* to account for geographic information

In this section, we first recall the reconciliation model followed by *Mowgli* (Doyon et al., 2010).

Only rooted parasite and host trees are considered; their leaf nodes (tips) are each labelled by a taxon name. The host tree is dated, meaning that either each branch length represents an amount of time (the tree is thus ultrametric) or that the age of each internal node is provided (e.g., in million years). Internal nodes usually have two descendants, but an internal node can also have a single child when the evolution of an ancestral lineage living a relatively long period of time is decomposed into a set of consecutive time periods called *slices* (see Figure 3 of *Mowgli's* manual). This slicing of branches is a transparent artefact that leads to reconciliation methods achieving fast computing times while still ensuring time consistency of host switches (see Doyon et al., 2010; Jacox et al., 2016; Libeskind-Hadas & Charleston, 2009).

Let  $P$  and  $H$  denote respectively a parasite and a host tree,  $x, x'$ ,  $x_p$ ,  $x'_p$  denote nodes of  $H$ , while  $u$  and  $u_p$  will denote nodes (or extant species) of  $P$ . Reconciliation algorithms usually consider each current and ancestral host to be associated with one or several specific parasites at any time (e.g., in *Mowgli*, *TreeMap*, *Jane*). However, the identity of the host can vary over time, for example after a *host switch*. This evolutionary event is one of the four types of events considered in cospeciation studies:

1. A *host switch* (T event), occurs when a parasite lineage from a source host is transferred to a destination host. The transfer of the parasite must be time-consistent; that is, the “sending” branch ( $x_p, x$ ) and the “receiving” branch ( $x'_p, x'$ ), where the host switch is mapped must belong to the same time slice.
2. A *cospeciation* (S event) happens when the speciation of a parasite shortly follows or coincides with the speciation of its host. *Mowgli* considers this as a joint speciation of both the parasite and its host.
3. A *within-host speciation*, also known as a duplication (D event), models a speciation of a parasite  $u$  of  $P$ , where both descendant species continue to live onto the host that  $u$  lived on. This is represented by  $u$  evolving along a branch ( $x_p, x$ ) of  $H$  and then splitting into two new lineages along ( $x_p, x$ ).
4. A *parasite loss* (L event) occurs when a parasite lineage goes extinct, while its host persists.

An illustration of these events can be found *Mowgli's* manual.

*Mowgli* also sometimes considers combinations of events to speed up computations. An SL event represents a parasite loss (L) occurring shortly after a cospeciation (S): this corresponds to a situation where an ancestral parasite evolves in association with an ancestral host; then, both speciate but only one of the host new lineages is associated with a parasite lineage, the other host lineage losing its associated parasite at some point in time after the speciation. A TL event occurs when a parasite  $u$  evolving on a branch ( $x_p, x$ ) is lost (L) on this branch shortly after having switched (T) to another host ( $x'_p, x'$ ). This corresponds to a parasite lineage being associated with the start of a branch in the host tree, being transferred and then disappearing from the initial host branch (see *Mowgli's* manual for an illustration).

As explained above, accounting for geographic information can lead to more realistic diversification scenarios. We first integrate such information by assigning a set of *areas* to each node of *P* and *H*. For an extant taxon, this means that a population of the corresponding species is reported to live in *each* of the assigned areas. In contrast, when an internal taxon is assigned to one or several areas, this means that populations of this now extinct taxon are inferred to have lived back in time in one or several of these geographical zones.

To compute biogeographically meaningful reconciliations between the *P* and *H* trees, specific constraints have to be implemented in reconciliation algorithms. We detail below how we model these constraints in the context of the four D/T/L/S events or combinations thereof. First, note that areas of a node and its parent in the host or parasite tree can be different due to dispersal and vicariance events. In the reconciliation process, the areas assigned to a branch between host nodes  $x_p$  and  $x$  are those of  $x_p$  together with those of  $x$ , and for the whole period between these two nodes. Indeed, a population of the host species resulting from speciation  $x_p$  can change area before reaching speciation  $x$ , and we have no information to know at which point in time this happened along the branch.

Considering nodes of the trees, we denote by  $area(x)$  the set of geographic areas where an extant species  $x$  is observed (at the tip of a tree). Areas proposed (most often *inferred*) for an internal node  $x$ , that is for an extinct species, are also denoted  $area(x)$ . However, as indicated above, the meaning is somewhat different as  $area(x)$  represents in this case the set of areas where  $x$  *could* have lived. Because of the uncertainty in the historical biogeography inferences, we do not enforce that  $x$  lived in each of these areas. Similarly, considering branches  $(x_p, x)$  of the *H* tree,  $area(x_p, x)$  denotes the set of areas where the species might have lived during this period: this is the union of  $areas(x_p)$  and  $area(x)$ . Note that each area in which exactly one of the two species  $x$  and  $x_p$  is present corresponds to a migration or extinction event that has occurred along this branch. In addition, only  $(x_p, x)$  branches being one slice high are considered for *H*, as *Mowgli* operates on this level of detail.

We now detail which geographic constraints apply so that the reconciliation between a parasite tree *P* and a host tree *H* is geographically consistent. Recall that a reconciliation is a mapping of *P*'s nodes and branches onto those of *H*.

1. An extant parasite  $u$  can be mapped onto an extant host  $x$ , only if  $area(u) \subseteq area(x)$  (Figure 1a). If this constraint is not fulfilled, then *Mowgli* cannot compute a reconciliation.
2. We allow the mapping of an ancestral parasite  $u$  at a speciation node  $x$  in the host tree, only if  $area(u)$  and  $area(x)$  have a nonempty intersection, that is when there is at least one area where the parasite and the host were able to meet (Figure 1b).
3. A parasite node  $u$  can be mapped into a branch  $(x_p, x)$  of *H* due to a duplication or host switch event (Figure 1c), and in those cases also, we require that  $area(u) \cap area(x_p, x) \neq \emptyset$ . Note that this

constraint does not prevent parasite dispersal events during host switches.

4. If a branch  $(u_p, u)$  of the parasite tree is mapped for all or part of it onto a host branch  $(x_p, x)$  (Figure 1d), then we require that  $area(u_p, u) \cap area(x_p, x) \neq \emptyset$ .
5. Last, if a branch  $(u_p, u)$  of the parasite is going through a node  $x$  of the host tree (which happens when the host speciates into two descendant hosts but the parasite sticks to only one of them—an SL event), then  $area(x)$  and  $area(u_p, u)$  must have common elements (Figure 1e).

Note that when part of the reconciliation mapping traverses an artificial node  $x$  in *H*, then no particular constraint applies locally: the possibility of such a scenario is directed by constraints ensured with respect to the branch  $(x_p, x)$  of *H* to which  $x$  belongs.

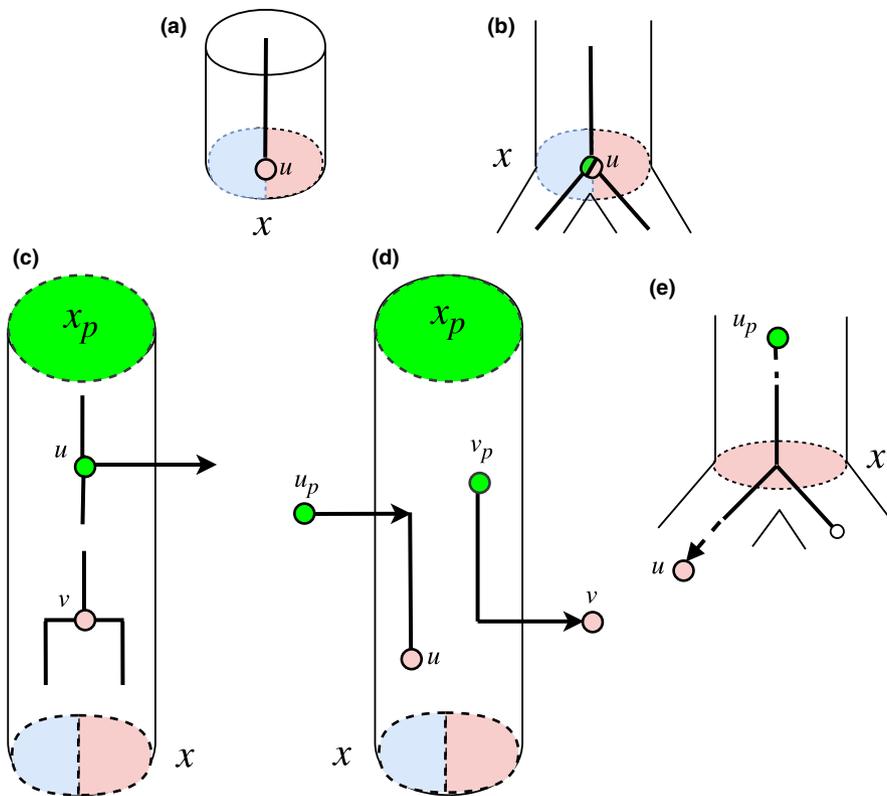
When respecting the above constraints, *Mowgli* will propose a scenario that is geographically consistent. This scenario can have a higher cost than those obtained when not accounting for geographic information. This simply stems from the fact that the search space contains geographically inconsistent scenarios that are possibly less costly. *Mowgli*'s extension described above finds the less costly scenario among those that are geographically consistent.

## 2.2 | *SylvX*'s new functionalities

We extended the *SylvX* editor to visualize current and ancestral geographic areas of hosts and symbionts. Pie charts can be used to display alternative areas for each node of the tree and/or the reconciliation. Area colour sets can be dynamically updated and tuned using the hue, saturation and value scales. Thresholds are available to simplify views. *SylvX* also contains a new tool in the *Annotation* panel to highlight reconciliation parts that do not respect geographical constraints (when such constraints have not been enforced when computing the reconciliation). To achieve this, users can load a specific annotation file generated by *Mowgli* (namely, constraintsPBM.csv).

## 2.3 | Implementation

*Mowgli* takes as input a "host tree" and a "parasite tree" stored in files with a Newick format. A list of nodes with their geographic areas (or other annotations) can be given in the same files. Biogeographic inferences typically generate probability or likelihood values for each character state (area) at each node. *Mowgli* can accept a single area or a set of areas at each node. To run *Mowgli* and obtain a reconciliation respecting geographical constraints, the `-a` flag must be added in the command launching the program. Adding the `-y` flag instead computes a reconciliation independently of the indicated constraints but pinpoints the places where the mapping violates these constraints (in mapping.mpr and constraintPBMs.csv files, see the manual for details). Users can then identify inconsistencies between the most parsimonious reconciliations and the hosts and parasites respective biogeographic histories.



**FIGURE 1** Description of how geographical constraints are handled by the *Mowgli* software. Plain lines and nodes represent branches and nodes of the parasite tree, while cylinders and dashed ellipses represent branches and nodes of the host tree. The colours of a node correspond to geographical areas, and these areas are observed (hence enforced) for extant taxa but inferred for ancestral nodes. (a) The parasite tip  $u$  can be mapped to a tip  $x$  of the host tree if the areas of the host contain all areas of the parasite. (b) *Mowgli* accepts that a parasite node  $u$  cospeciates with a host at a node  $x$ , if the two nodes share at least an area. Here, it was inferred that the ancestral parasite  $u$  lived in green and/or red areas, but cospeciated with a host  $x$  that lived in blue and/or red areas, we conclude that  $u$  lived only in the red area at this time and that  $x$  lived at least in the red area. (c) To map an ancestral parasite inside a branch  $(x_p, x)$ —to represent the source of a host switch (upper part of the figure), or a duplication of the parasite (lower part)—*Mowgli* requires that the parasite has potentially lived in an area common to  $x_p$  or  $x$ . In this example,  $u$  shares an area with  $x_p$  and  $v$  shares an area with  $x$ . (d) To map a branch  $(u_p, u)$  of the parasite tree inside a branch  $(x_p, x)$  of the host tree, *Mowgli* requires that the parasite mapped on the host branch ( $u$  in the left part of the figure showing the destination of a switch and  $v_p$  in the right part showing the departure due to a switch) has potentially lived in any area assigned to node  $x_p$  or to node  $x$ . This is the case here for node  $u$  that is indicated as having lived in the red area (also assigned to  $x$ ) and for  $v_p$  assigned to the green area, also proposed for  $x_p$ . Note that mapping  $v_p$  into  $(x_p, x)$  would have also been correct if  $v_p$  had been assigned to the red area, indicating that it changed from the green to the red area, together with its host, before switching to another host (this is allowed as  $x$  has a red area). (e) When a parasite lineage  $(u_p, u)$  living on an ancestral host remains with one descending child of this host after its speciation at node  $x$ : *Mowgli* requires that the area at which the host speciation occurred is also found among the areas inferred for  $u_p$  or  $u$ . The mapping in this example indicates that the parasite changed area with its host, before the host speciation event

*SylvX* takes a host tree in Newick format with node *id* numbers and a reconciliation (with symbiont tree node *id*). The host tree (outputSpeciesTree.mpr) and a reconciliation obtained with *Mowgli* (in the FullReconciliation.mpr file) can be directly imported into *SylvX*. The latter also supports input files from other reconciliation software, for example ecceTERA (Jacox et al., 2016). Annotation files for the host and parasite phylogenies giving node information can be imported in a CSV format. As many annotations as needed can be added in the annotation files, and it is up to the user to choose which ones to plot onto the species tree and the reconciliation map through *SylvX*'s interface.

To seamlessly pass a user annotation file in csv format into both *Mowgli* and *SylvX*, we provide a *Perl* script that can be run through the command line to: (a) obtain tree node identifiers that will be

used by both programs and (b) merge input trees and corresponding annotations files into *Mowgli*'s input format. Files can be generated so that a single (most likely) ancestral range can be specified or alternative geographic areas can be assigned to all nodes (see Supporting Information Material S1 for a description of the full procedure to generate files, set a threshold value above which to keep alternative areas and perform a complete analysis).

### 3 | WORKED EXAMPLE

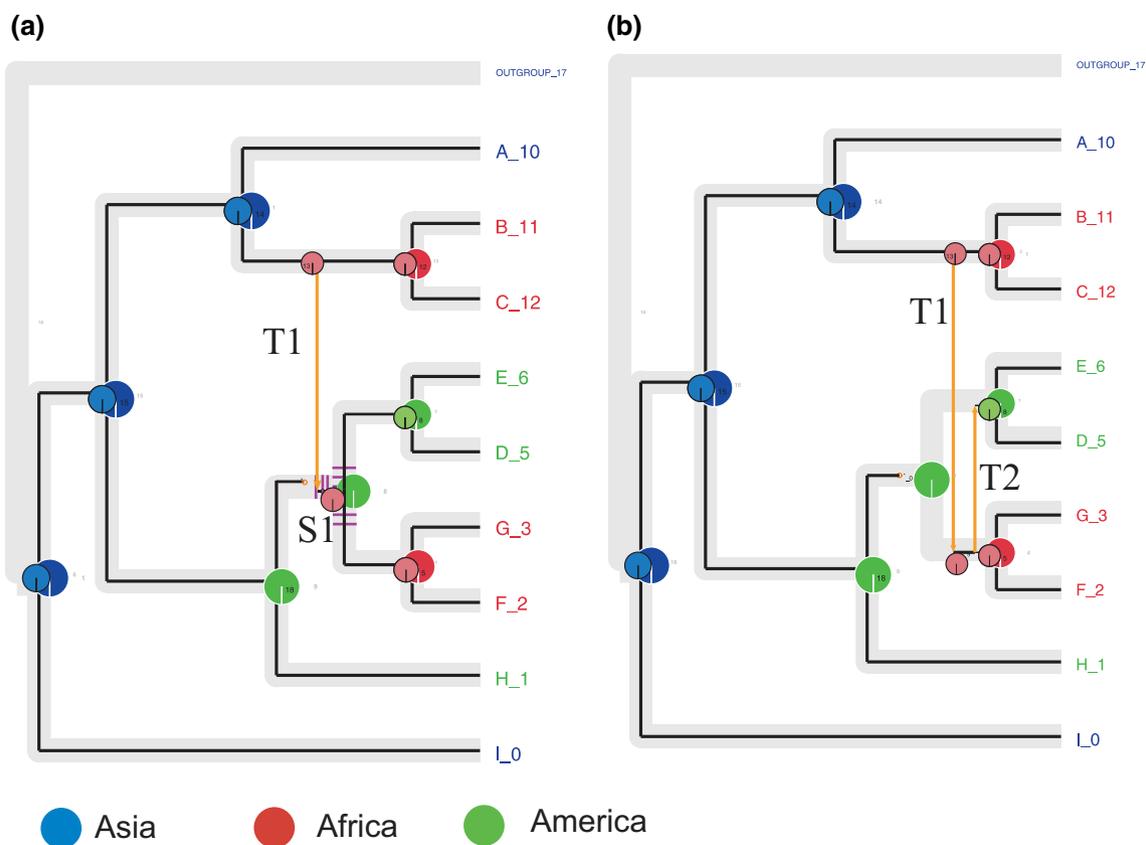
#### 3.1 | Data sets

To demonstrate the method and its utility, we tested it on two data sets. We first created a mock data set: two phylogenetic trees with

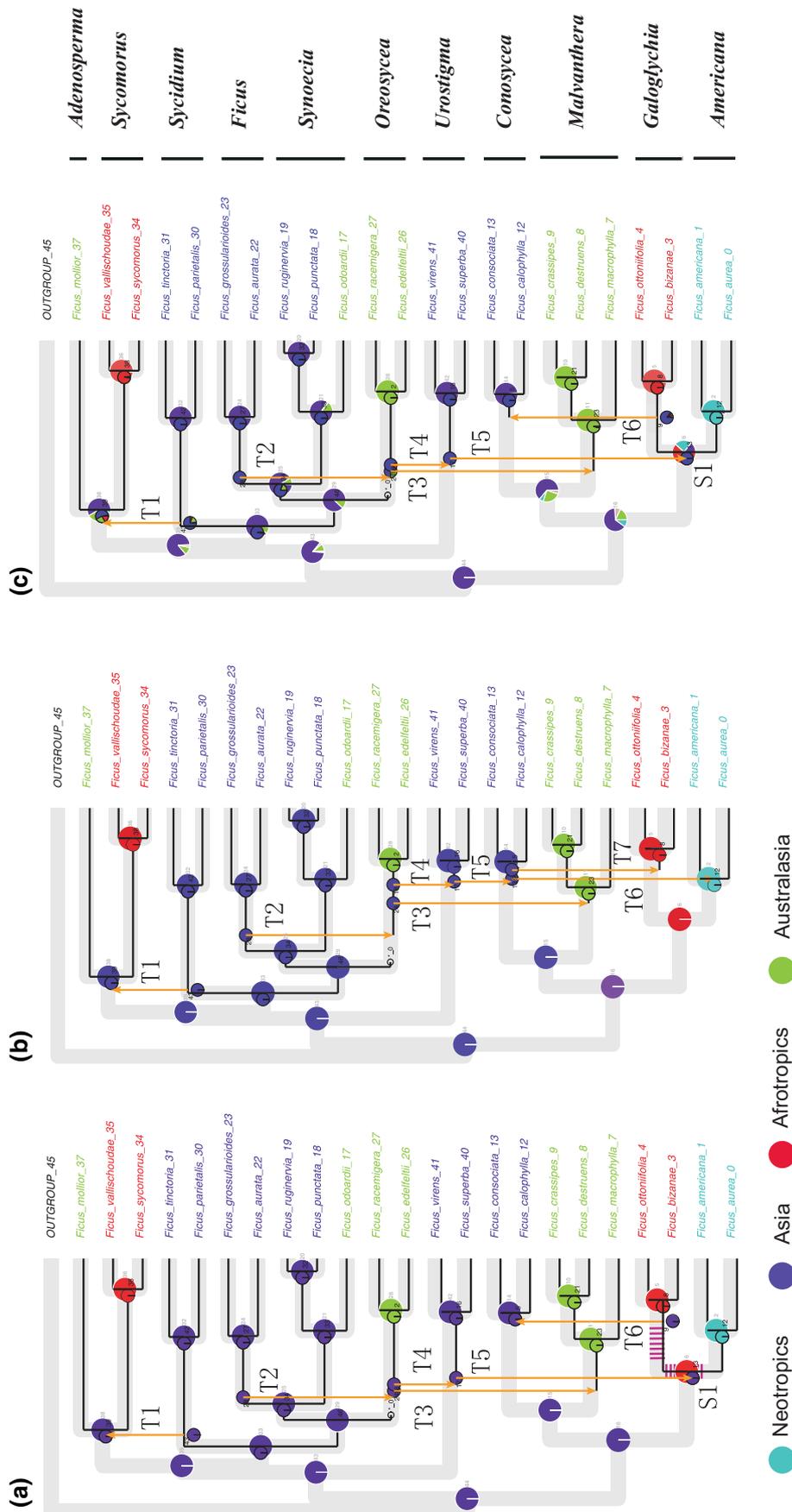
nine tips for a hypothetical host/parasite interaction in which extant and ancient geographic areas for each lineage are informed. The data set was generated by hand so that (a) present-day geographic areas of associated taxa are consistent (i.e., hosts and associated parasites live in the same area); (b) the two phylogenies are not perfectly parallel but show some cospeciation events; and (c) some geographic locations at nodes that we would like to cospeciate do not coincide in the parasite and host phylogenies. We ran *Mowgli* on this data set successively with and without enforcing geographic constraints using in both cases the default parameters (cost 0 for a cospeciation, 1 for a loss and 1 for a host switch, 1 for duplication, not enforcing the root of the parasite tree to be mapped on the root of the species tree). To measure the impact of cost settings on the reconciliation scenarios, we ran this data set using alternative costs for host switches and losses.

As a second data set, we used a subset of the data from the latest phylogenetic investigation of figs (*Ficus*) and their pollinating wasps (Cruaud et al., 2012). For both partners of the association, biogeographic scenarios were available for phylogenies of 200 taxa. From the complete phylogenetic trees (available in <http://datadryad.org>, <https://doi.org/10.5061/dryad.hr620>), we derived two trees of

23 taxa each, that included a couple of representative species for each *Ficus* main taxonomic subdivision. We excluded one of the fig subgenera (*Pharmacosycea*) and its associated pollinators (*Tetrapus* spp.) whose phylogenetic positions are still debated. We have not tested our method on the total data set presented in Cruaud et al. (2012) as some uncertainties remain concerning the root of the phylogenetic trees, which could lead to spurious interpretations. The most likely ancestral geographic areas of each node were directly derived from the biogeographic reconstructions of Cruaud et al., 2012; obtained with maximum-likelihood optimization in Mesquite (Maddison & Maddison, 2008). We ran *Mowgli* on this data set with and without enforcing geographic constraints (using default event costs and not enforcing the root of the parasite tree to be mapped on the root of the species tree) and explored how these reconstructions shed light on the biogeographic history of the association. To investigate how uncertainty on ancestral geographic ranges impacts the reconciliation, we ran the reconciliation on the data set including alternative ancestral areas for both *Ficus* and their associated pollinators. For each node of the pollinator and the *Ficus* phylogenies, the geographic areas where proportional likelihood was above 0.15 were kept and assigned to their respective nodes.



**FIGURE 2** Results of the reconciliations obtained on a simulated data set with default cost settings: (a) without enforcing geographic constraints (8 cospeciation events, 1 transfer, 1 loss), purple dashed branches indicate parts of the reconciliation where geographic constraints are not fulfilled (b) when enforcing geographic constraints (7 S, 2 T, 1 L). In both cases, the big pie charts correspond to the host ancestral geographic areas while small pie charts correspond to the symbiont ancestral geographic areas. The leaves of the species tree are also coloured according to the current geographic distribution of the associates. Annotations files given for the host tree and the symbiont tree specified a single most likely area at each node



**FIGURE 3** Results of the reconciliations inferred by Mowgli on the fig/fig wasp data set with default cost settings: (a) using a single most likely area for ancestral species and without enforcing geographic constraints (events: 17 S, 6 T, 1 L), purple dashed branches indicate parts of the reconciliation where geographic constraints are not fulfilled; (b) using a single most likely area when enforcing geographic constraints (events: 16 S, 7 T, 1 L). The leaves of the phylogenetic trees are coloured according to current geographic distribution of the associates. In both cases, big pie charts correspond to the *Ficus* ancestral geographic areas, small pie charts correspond to the pollinator ancestral geographic areas; (c) reconciliation obtained when several alternative ancestral areas are considered, namely those with probability > 0.15 (Events 17 S, 6 T, 1 L). Sections of the pies are proportional to the probability of the associated states. *Ficus* taxonomic subdivisions are reported on the right side of the figure

## 4 | RESULTS

Figure 2 represents the reconstruction obtained on the mock data set. When not taking geographic constraints into account (Figure 2a), a cospeciation event at a node where the two associates do not live in the same area was retrieved (node S1 of the host tree in Figure 2a). The transfer T1 preceding this cospeciation event is also geographically impossible as it suggests a dispersal (the donor host lives in Asia or Africa, and the receiving host lives in America) while the parasite actually stays in Africa. The scenario obtained when enforcing geographic constraints is more costly (Figure 2b): it entails one more transfer and consequently one less cospeciation event but is biologically more realistic. When using different cost vectors (i.e., using a cost of three for losses), the reconciliation where geographic constraints are not taken into account includes additional transfers to avoid losses (Supporting Information Figure S2a); those are all geographically inconsistent. The reconciliation with geographic constraints also changes (Supporting Information Figure S2c) and necessitates five transfers to ensure geographic consistency of the diversification events in hosts and parasites without inferring any parasite losses. When we increased the cost of transfers (cost  $T = 10$ , Supporting Information Figure S2b), the reconciliation without geographic constraints infers several early duplications and losses to avoid a costly transfer. On the other hand, the results of the reconciliation under constraints (Supporting Information Figure S2d) did not change comparatively to the one obtained with default cost settings. Hence, in this particular case, adding biological constraints into the reconciliation process stabilizes the reconciliation and makes it less dependent on cost settings.

On the fig/fig wasp data set (Figure 3), not accounting for geographical constraints leads to geographic inconsistency in one node (cospeciation S1 in the host tree of Figure 3a). The transfer that precedes it (T5) is impossible, and the mapping of the fig wasp phylogeny onto the fig phylogeny from node S1 to event T6 is geographically inconsistent (Figure 3a). Enforcing geographic constraints when a single (most likely) area is specified for each node generates a reconciliation scenario that is more costly (Figure 3b, one more transfer is necessary to reconcile the two phylogenies) but coherent with the figs and the fig wasp biogeographic histories. This scenario suggests that the fig wasps independently colonized figs in the Neotropics and in the Afrotropics through two distinct host switches from Asia rather than accompanied the speciation of their hosts, as was suggested by Figure 3a (and node 29 of figure S12 in Cruaud et al., 2012). The annotation of ancestral geographic areas on the reconciliation map also shows that host switches occurred in both “sympatric” settings (within the same geographic areas as broadly defined in our data set) and allopatric settings (i.e., host switches occur between two geographically distant hosts). Overall, four switches of seven occurred in sympatry (T1, T2, T4 and T5), while the remaining three switches (T3, T6 and T7) correspond to long-distance dispersal events (Figure 3b). Adding uncertainty in ancestral geographic range generates a reconciliation that matches the one obtained without constraint

(Figure 3c), as geographic areas of node S1 of the host figs now includes Asia among its potential geographic areas. This matches the ancestral geographic area of the inferred associated fig wasps. In that scenario, a single host switch is associated with a long dispersal event of the fig wasps (T3: from Asia to Australasia), all other host switches occur in sympatric settings (within Asia), and fig wasp geographic range evolution merely mirrors the one of their hosts.

## 5 | DISCUSSION

We provide here significant extensions for a reconciliation tool (*Mowgli*) and a visualization tool (*Sylvx*) to infer codiversification scenarios that, for the first time, can take the historical biogeographies of the associated lineages into account. The extension of the *Mowgli* software precludes geographic inconsistency during the reconciliation process. The resulting reconciliations can then be visualized and edited in the *Sylvx* updated graphical interface that now integrates annotations of ancestral nodes. *Mowgli* is already one of the few time-consistent efficient methods that build optimal reconciliations. With the integration of geographic constraints in its algorithm, this tool now provides more realistic codiversification scenarios than other reconciliation methods. Producing biologically realistic scenarios can ease their interpretation. In addition, geography-aware reconciliations can reveal whether host switches occur in sympatry or whether they are associated with dispersal events of the symbionts/parasites: this helps with the unravelling of evolutionary processes underlying host switches.

In the particular example of the fig/fig wasp interaction presented here, several geographic inconsistencies resulted from the run of *Mowgli* without asking the program to account for geographical constraints. One of them concerns cospeciating nodes in the analysis (Figure 3a) and might actually point out some ambiguity in the biogeographic history of the *Ficus* hosts. According to the inference conducted in Cruaud et al. (2012), the most likely area for the common ancestor of Neotropical figs (belonging to the *Americana* section) and Afrotropical figs (belonging to the *Galoglychia* section) is Africa, while the proposed cospeciating pollinators lived in Asia (S1; Figure 3a). To respect geographic consistency (when only the most likely area is kept for each ancestral species, Figure 3b), our geography-aware reconciliation suggests that the current association of fig wasps with *Galoglychia* in Africa, and *Americana* in the Neotropics, is the result of two independent switches (Figure 3b, events T6 and T7) of the pollinators from an Asian fig ancestor (the ancestor of the *Conosycea* figs). However, the biogeographic analysis of Cruaud et al. (2012) also suggested that the node S1 of *Ficus* could be situated in Asia (though with a much lower likelihood than the Afrotropics). When specifying alternative geographic areas (Figure 3c), including Asia for the conflicting node in the *Ficus* phylogeny, we obtain a reconciliation that matches the one obtained without constraints (implying one less transfer and one more cospeciation event). This result suggests that the common ancestor of the African figs of the

*Galoglychia* section and the new world figs from the *Americana* section could indeed have been located in Asia. Under the latter scenario, most of the switches between host figs happen in sympatric settings. We will not further discuss the biogeographic history of the fig/fig wasp association, as the purpose of our study is not to explore alternative scenarios for this association. The above discussion mainly demonstrates the utility of our method in revealing inconsistencies between biogeographic scenarios and a cospeciation hypothesis and proposing alternative scenarios that conciliate both. As in all ancestral character state inferences that rely on present-day data, biogeographic reconstructions entail some uncertainty. In particular, they are highly sensitive to missing data (species that have not been sampled and/or extinct species). Computing and visualizing reconciliations using different biogeographic scenarios can help identify which alternative ancestral areas are the most likely when several are proposed in a reconstruction (i.e., the areas that are occupied simultaneously by host and their associates). One strategy could consist in computing a reconciliation with the most likely areas only and then include less likely areas into the reconciliation process to see how the scenarios change. This could also help identifying which parts of the reconciliation are constant under alternative biogeographic hypotheses.

## 5.1 | Perspectives

The tools developed in this study can be applied to all interspecific interactions for which biogeographic scenarios are available for both partners. Fast developments in sequencing technologies are generating more accurate and more exhaustive phylogenies, and methods in historical biogeography are improving. Therefore, we can hope that numerous data sets will be available in the near future and cospeciation could be tested on more systems (Cruaud & Rasplus, 2016). For instance, robust phylogenies and biogeographic scenarios are now available for groups of lice that have been model systems in coevolutionary studies (Boyd et al., 2017). Once comprehensive phylogenies of the hosts are available, our method could be used to better understand the geographic context of host switches in this model system. Geography-aware reconciliation could also be applied to explore the diversification history of the numerous parasitic wasps that are part of the microfauna exploiting figs: several lineages of parasitic wasps have been shown to partly cospeciate with their host figs (Jousselin, Van Noort, Rasplus, & Greeff, 2006; Jousselin et al., 2008) and biogeographic scenarios for some lineages are available (Cruaud et al., 2011). These developments could also be applied to specific sections of the *Ficus* genus to shed light on their complex biogeographic histories (e.g., *Urostigma* section that has experienced several dispersal events between Africa and Asia, Chantarasuwan, Rønsted, Kjellberg, Sungkaew, & van Welzen, 2016). Other nursery pollination/mutualisms such as the interaction between *Yucca* and their pollinating moths are also good candidates for including geographic constraints into coevolutionary scenarios, as studies have questioned the respective role of geography and host-plant

association in driving the diversification of *Yucca* moths (Althoff, Segreaves, Smith, Leebens-Mack, & Pellmyr, 2012). Other interesting applications are plant/pollinator systems (Hutchinson, Cagua, & Stouffer, 2017), parasitoid/host insect associations (Deng et al., 2013; Wilson et al., 2012), herbivorous insect/plant interactions (e.g., McLeish, Crespi, Chapman, & Schwarz, 2007; Percy, Page, & Cronk, 2004) and various vertebrate/parasite associations (e.g., Badets et al., 2011; Bentz et al., 2006; Weckstein, 2004) for which researchers have investigated the relative role of geography and biotic interactions in shaping cophylogenetic signals.

Furthermore, the approach presented in this study does not only apply to geographic information and could be extended to other biological traits. For instance, in systems where the species are partitioned into different habitats (e.g., forest canopy species vs. savannah species), geographic areas could be replaced by traits related to the ecological niches; constraints that are similar to the ones applied for geography could then be easily transferred. First inferring ancestral host and symbiont habitats and then running "Mowgli with constraints" would result in constraining cospeciation events and host switches to associates sharing the same ecological habitats. In a similar way, the respective climatic niches of associated organisms could also be used when parasite (or symbiont) distributions are known to be strongly constrained by thermal tolerance (see Singh et al., 2017; for a recent study showing that climatic conditions influence the patterns of association between fungi and their algal partners). In many specialized interactions, such as host/obligate bacterial endosymbionts (e.g., Jousselin, Desdevises, & Coeur d'acier, 2009; Rosenblueth, Sayavedra, Samano-Sanchez, Roth, & Martinez-Romero, 2012) or host/viruses associations (Garamszegi, 2009; Ramsden, Holmes, & Charleston, 2009), inferring ancestral character states for some ecological traits for the "symbiotic" lineages (the parasite) independently of their hosts is not always straightforward. However, the evolution of these obligate associations and their maintenance are still governed by some phenotype matching between the partners. For instance in host/bacterial symbiont associations, the metabolic complementarity of the host and the symbiont (Zientz, Dandekar, & Gross, 2004) could be reconstructed and used to constrain the reconciliations. In host/virus associations, information about the host immune system and viruses adaptations could be used (Longdon, Brockhurst, Russell, Welch, & Jiggins, 2014). The extension of *Mowgli* proposed here could probably be adapted to fit the biological properties of these associations.

Besides the new functionality implemented in *Mowgli*, the concomitant update of *SylvX* allows users to compare the ancestral states for any character of the hosts and/or the symbionts. This can help with the interpretation or reconciliations by replacing them in their biological context. One of the most useful functionalities of *SylvX* is now the ability to visualize whether host switches are associated with evolutionary transitions in character states in both the parasite and the host. It can therefore help understanding the biological processes that are associated with these transfers. Mapping characters of the associates throughout the reconciliation can also help visualizing whether there is correlated trait evolution in hosts

and parasites. Until now, such correlations could only be investigated on one of the associate phylogenies (e.g., Joussetin, Rasplus, & Kjellberg, 2003; Sorci, Skarstein, Morand, & Hugot, 2003). Looking at simultaneous transitions in character states in both partners throughout a host/parasite reconciliation might reveal the coadapted traits that constrain the association.

In conclusion, we provide a framework that can integrate the character histories of the associates into the reconciliation process. It can take into account uncertainty in the character states and facilitates the recovery of biologically realistic scenarios. It can also shed light on character history inferences by pointing out inconsistencies between the character states of the two associates on the reconciliation map. The new developments made in *SylvX* facilitate these interpretations. A more integrative approach than the one presented here would co-optimize the reconciliation and the biogeographical inference simultaneously. However, this would require the use of the same optimization criterion for both inferences and setting adequate parameters for these very different processes in a single model. When conducted, this work should probably rely on maximum-likelihood optimization as in the ALE reconciliation software (Szöllösi et al., 2012). For now, we believe that the use of “constraint-aware” reconciliations is preferable to current practices that elaborate ad hoc narratives once the reconciliations are obtained and compared with the character histories of the associates.

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## SOFTWARE AVAILABILITY

Mowgli is available at [http://www.atgc-montpellier.fr/Mowgli/with\\_manual](http://www.atgc-montpellier.fr/Mowgli/with_manual), example files and *GeoRecHelper* script, it runs on Linux and Mac (OSX) computers; *SylvX* is available at [www.sylvx.org](http://www.sylvx.org) with manual and example files and can be installed on any platforms.

## AUTHOR CONTRIBUTIONS

V.B., J.P.D. and E.J. designed the study. V.B. and J.P.D. developed *Mowgli*, F.C. developed *SylvX*. V.B. and E.J. wrote the manuscript with contributions of F.C.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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