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Oral Fairy Tale or Literary Fake? Investigating the Origins of Little Red Riding Hood Using Phylogenetic Network Analysis

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Abstract

The evolution of fairy tales often involves complex interactions between oral and literary traditions, which can be difficult to tease apart when investigating their origins. Here, we show how computer-assisted stemmatology can be productively applied to this problem, focusing on a long-standing controversy in fairy tale scholarship: did Little Red Riding Hood originate as an oral tale that was adapted by Perrault and the Brothers Grimm, or is the oral tradition in fact derived from literary texts? We address this question by analysing a sample of 24 literal and oral versions of the fairy tale Little Red Riding Hood using several methods of phylogenetic analysis, including maximum parsimony and two network-based approaches (NeighbourNet and TRex). While the results of these analyses are more compatible with the oral origins hypothesis than the alternative literary origins hypothesis, their interpretation is problematised by the fact that none of them explicitly model lineal (i.e. ancestor-descendent) relationships among taxa. We therefore present a new likelihood-based method, PhyloDAG, which was specifically developed to model lineal as well as collateral and reticulate relationships. A comparison of different structures derived from PhyloDAG provided a much clearer result than the maximum parsimony, NeighbourNet or TRex analyses, and strongly favoured the hypothesis that literary versions of Little Red Riding Hood were originally based on oral folktales, rather than vice versa.

1. Introduction

Recent years have witnessed a boom in computational approaches to the reconstruction of literary traditions, fuelled by the adoption of phylogenetic techniques from evolutionary biology and the development of custom-made software for textual analysis (Howe et al., 2001; Roos & Heikkilä, 2009). So far, research in this field has focused on the transmission histories of hand-copied manuscripts, where the accumulation of errors and occasional innovations can be modelled as a branching process analogous to the diversification of biological lineages by descent with modification. Recently, it has been argued that a similar approach can shed light on the evolution of oral traditions, such as folktales (Tehrani, 2013), legends (Stubbersfield & Tehrani, 2013) and myths (d'Huy, 2013). Although these stories are not literally copied in the way that manuscripts or DNA sequences are, their basic plot elements, motifs, characters and symbols exhibit clear evidence of both fidelity of transmission as well as cumulative change through time. Recent case studies (Tehrani, 2013) demonstrate that careful analyses of these features make it possible to reconstruct deep and robust stemmata, which can in turn yield potentially crucial insights into the origin and development of oral tales.

One of the key issues in this area concerns the complex interactions between oral and literary traditions, which are often difficult to disentangle. For example, it is well known that, historically, many so-called fairy tales (i.e. traditional short stories containing fantastical or magical elements) have been adapted by writers inspired by oral story-tellers and vice versa. In such cases, it can be extremely problematic to establish in which medium a given tale originated. While most folklorists have tended to assume that fairy tales are rooted in oral tradition, some scholars have argued that they may in fact be derived from written texts. Most notably, Ruth Bottigheimer (Bottigheimer, 2002, 2010) proposed that fairy tales are a primarily literary genre that was invented by the sixteenth century writer Giovanni Francesco Straparola and subsequently popularised by other authors such as Basile, Perrault and the Brothers Grimm. While these authors presented their stories as though they were borrowed from the tales told by common folk, Bottigheimer suggests this was simply a stylistic ruse, and that the direction of transmission was much more likely to be the other way around. In support of this point, she highlights that the earliest literary versions of fairy tales were written centuries earlier than the supposedly more authentic oral versions collected by folklorists. Bottigheimer's controversial thesis has been rejected by most experts (Ben-Amos, Ziolkowski, Silva, & Bottigheimer, 2010), who point out that absence of evidence hardly constitutes evidence for absence, especially given that oral traditions, by definition, lack a written record. However, by the same token, nor can it be proved that oral fairy tales predate the earliest written versions. In this paper, we show how techniques developed in computer-assisted stemmatology can help break this impasse, and shed new light on the missing links between oral and literary traditions in fairy tales.

Our case study focuses on a tale whose origin has long been the subject of intense controversy: Little Red Riding Hood. The tale, which is classified as ATU 333 in the Aarne-Thompson-Uther (ATU) Index of International Tale Types, famously tells the story of a young girl who is attacked by a wolf disguised as her grandmother. There are numerous theories about the source of the tale, from pre-Christian sun myths (Saintyves, 1989) or medieval coming-of-age rites (Verdier, 1978) to Chinese folk tradition (Haar, 2006). While these ideas remain difficult to substantiate, the modern tradition of Little Red Riding Hood/ATU 333 can be traced back to 1697, when the first classic version of the story, *Le Petit Chaperon Rouge*, was published by the French author Charles Perrault in his collection of purportedly traditional stories, *Histoires ou Contes du Temps Passé* (Tales of Past Times) (1697). A second classic version of Little Red Riding Hood (*Rotkäppchen*) was published in 1813 in the first volume of Jacob and Wilhelm Grimm's *Kinder und Hausmärchen* (Children's and Household Tales) (1812). In this version, unlike Perrault's, Little Red and her grandmother are rescued by a passing huntsman, who slices open the villain's stomach and sews it up again with stones. Although, like the other tales in that volume, Rotkäppchen was ostensibly collected from ordinary German peasant folk, Grimm scholars have established that the brothers' source for the tale was actually an educated woman of French-Huguenot descent named Marie Hassenpflug, who was almost certainly familiar with Perrault's enormously popular *Contes* (Zipes, 1993).

While the Perrault and Grimm tales provided the model from which all subsequent literary Little Red Riding Hoods are derived, the origins of the oral tradition of ATU 333, and its relationship to these two “classic” versions, are much less well understood. Most folklorists believe that Perrault based his tale on a traditional French werewolf tale, probably from his mother’s native region of Touraine, which was the site of a series of werewolf trials in the sixteenth and seventeenth centuries (Zipes, 1993, p. 20). It is claimed that variants of the tale survived into the nineteenth and twentieth centuries in the oral literatures of south-east France, the Alps and northern Italy (Delarue, 1951; Rumpf, 1989). These tales, commonly referred to as simply 'The Story of Grandmother' (following Delarue 1951) are typically more gory than Perrault's censored version – for example, the girl is tricked into eating some of her grandmother's remains. More importantly, rather than being a helpless victim, the girl typically outwits the wolf/werewolf by tricking him into letting her go outside to urinate. Although the provenance and antiquity of the tradition remains unknown, it has been suggested that it may go back to medieval times. This is supported by an eleventh century Latin poem by Egbert of Liége, which relates a local Walloon folktale in which a young girl encounters a wolf in the woods, and is saved by the supernatural protection afforded by her red tunic, a baptism gift from her godfather, (Ziolkowski, 1992). Although it is debateable as to whether or not this tale represents a direct ancestor to Little Red Riding Hood (Berlioz, 1991), the echo of common motifs like the young girl in the woods, the villainous wolf, the red outfit given to her by a relative, etc. certainly point to some kind of historical connection between them.

Nevertheless, other researchers are extremely sceptical that the oral variants held up by folkorists can be regarded as "independent" descendents of the pre-Perraudian oral tradition. Instead, they suggest that, like the Brothers Grimm version, these tales are more likely to be vernacular interpretations of published texts. For example, in an essay that strongly resonates with Bottigheimer's ideas, Hüsing (1989) writes that Little Red Riding Hood “represents one of the loveliest French literary tales, perhaps being the most successful fake that we have in the entire genre", which nonetheless lacks the characteristic stylistic features of authentic oral fairy tales (such as incompleteness). Similarly, Berlioz (1991) and, indeed, Bottigheimer herself (2010, p. 64), argue that there is no evidence to suggest that Little Red Riding Hood existed in oral tradition prior to the publication of Perrault's *Contes* at the end of the seventeenth century.

In this paper, we aim to shed more light on these issues by taking a quantitative stemmatological approach to investigate the relationships between oral and literary traditions of Little Red Riding Hood. Our study builds on Tehrani's (2013) recent phylogenetic analyses of the ATU 333 type tales, which investigated the relationships between oral European variants (plus Perrault and Grimm) to similar stories from other parts of the world, especially Africa and East Asia. Tehrani's study did not, however, address the question of whether Little Red Riding Hood originated in an oral or literary medium, nor did it examine interactions between the two traditions of ATU 333. Below, we outline how these issues were tackled in this study.

2. Materials

A total of 23 texts of Little Red Riding Hood were selected for analysis (see 'Sources' in Appendix A). To be clear, the aim of the analyses was not to produce a comprehensive stemma of the Little Red Riding Hood tradition – which would involve hundreds, if not thousands of texts – but to investigate a specific problem concerning the relationship of oral versions of the tale to literary versions. Specifically, we sought to test whether Perrault based his tale on a pre-existing oral tradition, or if both the oral and literary traditions derive from the classic versions of Perrault and the Grimms published in the seventeenth and nineteenth centuries respectively.

Our dataset included 12 Franco-Italian oral tales collected in the nineteenth and twentieth centuries that cover most of the major variations in the plot and character found in the folk traditions of these regions. For example, in some cases Little Red Riding Hood lacks her characteristic red hood and is simply described as a young girl. In many variants the protagonist outwits the villain to escape, but in others she is eaten. The character of villain, meanwhile, can take several forms, such as a wolf, witch or werewolf. In one group of Italian tales (three of which are included here) known as 'Catterinetta' – formerly categorized as a distinct subtype of ATU 333 (Aarne & Thompson, 1961) – the villain is actually the relative that the girl went to visit (usually an aunt or uncle). She/he takes revenge on the girl for eating the food that was in her basket and replacing them with cakes made from donkey dung. The dataset also included Egbert's 11th century poem, the classic versions of Little Red Riding Hood published by Perrault and the Brothers Grimm in the seventeenth and nineteenth centuries respectively, five examples of literary versions of Little Red Riding Hood from the late nineteenth and early twentieth centuries sampled from the deGrummond's Children's Literature Research Collection curated by the University of Southern Mississippi (http://www.usm.edu/media/english/fairytales/lrrh/lrrhhome.htm), and three oral variants from beyond the hypothesised ATU 333 cradle (two from Portugal and one from Lusatia in modern day Poland) that are thought to be based on literary texts, and which provide another useful point of comparison with the Franco-Italian oral versions.

Next, we constructed a matrix that coded the presence or absence of 58 traits (or, in phylogenetic parlance, "characters") identified in the 23 texts. The traits included features such as the red hood worn by the girl, the character of the wolf, the girl being eaten and so on (the full list of characters and the matrix are provided in Appendix A). The matrix only included traits that occurred in at least two tales, which might give clues about common ancestry. Traits that occurred in just a single text were excluded, since these would not be informative about relationships.

The matrix was analysed using several methods of phylogenetic/stemmatic reconstruction, each of which are described in the sections below. We predicted that, if the oral origins hypothesis is correct, then the literary tradition instigated by Perrault and also comprising the Grimms' *Rotkäppchen*, later published versions and oral copies from Portugal and Lusatia, should constitute a distinct lineage nested within a larger family of Franco-Italian folktales. Conversely, if the latter are derived from textual sources, they would be expected to comprise a lineage (or lineages) that split off from the literary tradition instigated by Perrault and continued by the Brothers Grimm. In the last analysis we introduce a method, PhyloDAG, that directly tests for ancestor-descendent relationships, while also allowing us to incorporate contamination between texts and/or oral traditions.

3. Phylogenetic Tree Analysis

Our first analysis employed the most-widely used method for reconstructing relationships among texts in stemmatology, maximum-parsimony (Howe et al. 2001). Maximum parsimony involves finding the tree(s) that minimises the number of evolutionary changes required to explain shared traits among a group of taxa (in this case, versions of Little Red Riding Hood) under a branching model of descent with modification. We carried out the maximum parsimony analysis in the software program PAUP 4.0* (Swofford, 1998). The results are shown in Figure 1.

Fig. 1 "Parsimony tree" about here.

The tree is rooted using the oldest text, Egbert's 11th century poem ("Latin"), as an outgroup. Under the oral origins hypothesis, Egbert's text represents the earliest known witness of the oral tradition of ATU 333 prior to Perrault, so it can be assumed that all the other texts (both oral and literary) are descended from a common ancestor of more recent origin. Under the literary origins hypothesis, Egbert's text would be excluded from the Little Red Riding Hood tradition, which is assumed to have originated six centuries later. Thus, both hypotheses would position Egbert's text as an outgroup with respect to the other texts.

The tree indicates that the literary versions of Little Red Riding Hood form a clade, or branch, that also includes the three oral "copies" from Portugal and Lusatia, as well as an Italian tale called *Three Girls*. Although the latter is technically a folktale, it is much closer to literary versions of ATU 333 than traditional versions of 'The Story of Grandmother' (for example, the girl is eaten and then subsequently cut out of the wolf's stomach), and is probably derived from published texts. The literary clade forms part of a larger grouping that comprises variants of the Franco-Italian tale 'The Story of Grandmother', but excludes variants of the Italian 'Catterinetta' tale (represented by *Catterinetta, Serravalle* and *UncleWolf*), which form a separate lineage splitting off at the root of the tree. Thus, as predicted by the oral origins hypothesis, the results of the maximum parsimony analysis suggest that the literary texts share a last common ancestor (LCA) of more recent origin than the LCA of the oral variants.

It is worth noting, however, that there are some inconsistencies between the tree and existing knowledge and theories about the Little Red Riding Hood tradition. For example, one of the literary variants (*Goldenhood*) and a Portuguese oral "copy" (*Consigliere*) form a clade that appears to be descended from a common ancestor of more ancient origin than Perrault. Since the literary tradition is known to have originated with Perrault, this anomaly can probably be attributed to an error of the maximum parsimony estimation, possibly as a consequence of contamination (or "reticulation" in phylogenetic jargon) between the literary and oral traditions. Contamination is likely to be common in fairy tale traditions as multiple oral and literary versions of a tale may circulate at the same time within and between geographical areas, and sometimes get mixed together (e.g. Tehrani 2013). Since the underlying model used in maximum parsimony analysis does not explicitly allow for horizontal transmission across lineages, it can sometimes erroneously interpret similarities that result from this process as primitive traits (i.e. the traits exhibited by the hybrid taxon are assumed to be inherited from an ancestral taxon that existed before the lineages leading to the two donor taxa split), thereby “dragging” highly contaminated variants deeper into the structure of the tree. This effect might similarly explain the position of one of the oral variants, *Joisten*, which is claimed to have borrowed traits from literary texts (Zipes, 1993, pp. 5-6), but appears in this tree to have split off from the LCA of the oral and literary tradition prior to the emergence of the latter. Another issue with maximum parsimony analysis is that it focuses solely on reconstructing collateral phylogenetic relationships (i.e. relationships based on common descent), rather than ancestor-descendent relationships. Consequently, it is not clear from the tree whether the position of Perrault should be interpreted as ancestral or collateral with respect to the other literary variants, while the position of the Grimm text is similarly ambiguous. These examples highlight the need to be cautious in drawing strong conclusions from the topology of the parsimony tree, or indeed other methods that assume a pure branching model of evolution.

4. Network Analysis

Phylogenetic networks provide an alternative approach to reconstructing cultural and biological evolution where relationships are not strictly tree-like. A number of methods for detecting different kinds of reticulation events have been proposed (Morrison, 2011). Many of the methods are specific to certain mechanisms, for instance, recombination and therefore not necessarily appropriate for modeling fairy tale traditions where the blending process is rather poorly understood and probably varies significantly from case to case.

Below, we present results from two popular network methods, NeighborNet and T-Rex. In addition, we present a new method, PhyloDAG, which is based on maximum likelihood analysis and allows generic directed networks or DAGs (directed acyclic graph).

We also apply a parametric bootstrap test to compare a number of network hypotheses obtained by the PhyloDAG method.

4.1 NeighborNet Analysis

A popular method for studying data that may involve reticulation is NeighborNet (Bryant & Moulton, 2003), (Huson & Bryant, 2006). In the terminology of Morrison (2011), NeighborNet is a data-display method. In other words, it does not attempt to construct a genealogical hypothesis that accurately represents the actual evolutionary history. Rather it attempts to represent the possibly conflicting phylogenetic signals in the data, so that non-tree-like structures may result either by actual reticulation or by other mechanisms such as evolutionary reversal or convergent evolution. Neither does the NeighborNet attempt to suppress statistically insignificant signals in the data which tends to result in very complex networks with a large number of non-tree-like structures.

Figure 2 shows the NeighborNet obtained for the data in our study by using the SplitsTree4 software[1]. The network shows similar clusters to the maximum parsimony analysis, distinguishing the literary variants (including the Portuguese and Lusatian oral copies) from Franco-Italian oral versions of ‘The Story of Grandmother’ and versions of the Italian ‘Catterinetta’ tale, which form a separate group. The "boxiness" of the network suggests probable lines of contamination within and between these sub-groups. However, the network has the typical problem associated with this method, which is that the middle part of the network is a very complex dense mesh of interconnected points that correspond to various weak conflicting signals in the data. Furthermore, all the most of the extant versions (the labelled points) are at the end of a long edge, suggesting that none of them (except perhaps one root node) are ancestors of the others. This makes is very hard to interpret the result in a way that would be informative for the questions we are presently considering. In particular, we can tell almost nothing from the network about the influence of Perrault and the Brothers Grimm on the oral tradition, or vice versa.

Fig. 2 "NeighborNet" about here.

4.2 T-Rex Analysis

Another technique from phylogenetics that can be used to model reticulation is T-Rex (Boc, Diallo, & Makarenkov, 2012). It starts from a tree structure and by comparing the pairwise distances computed from the data to the distances expected based on the tree, it identifies parts of the tree that fail to accurately match the distances in the data. In case certain groups of taxa are more similar to each other than the tree would lead us to expect, a reticulation edge may be introduced. The underlying tree structure is obtained by Neighbor-Joining (Saitou & Nei, 1987). The number of reticulation edges can be chosen by the user. We chose to include five of them in an attempt to discover the most significant contamination events.

The result of the T-Rex analysis is shown in Figure 3. The backbone phylogeny is largely similar to the parsimony tree, and indicates that the literary versions of Little Red Riding Hood form a branch that split from the lineage leading to modern oral variants of the traditional Franco-Italian tale ‘The Story of Grandmother’. Versions of the Italian tale ‘Catterinetta’ form a sister group to these tales. One notable difference between the T-Rex phylogeny and the parsimony tree is the position of *ThreeGirls*. As mentioned above, *ThreeGirls* is an Italian oral tale that shares notable features in common with the Grimms’*Rotkäppchen*. Whereas the parsimony analysis indicated that *ThreeGirls* was likely to be derived from literary texts (as per the Portuguese and Lusatian oral versions of ATU 333), T-Rex suggests that *ThreeGirls* is descended from an oral ancestor that preceded the literary tradition, but has been contaminated by the latter (N.B. although the reticulation edges in T-Rex are undirected, the well-documented influence of literary fairy tales – particularly the Grimms' *Kinder und Hausmärchen* – on European oral traditions (Zipes, 2013) support this interpretation). This is consistent with the NeighbourNet graph, which grouped *ThreeGirls* with oral variants, but indicated substantial conflict in the data surrounding its relationships to other tales. The T-Rex analysis proposed several other reticulation edges that suggest substantial mixing within regions between literary and oral traditions of ATU 333, notably between Perrault's classic text and French oral tales, and between the Italian variants of 'The Story of Grandmother' and 'Catterinetta'. More puzzlingly, the structure also suggests contamination from the Egbert's medieval poem and a modern literary version of Little Red Riding Hood (*CupplesLeon*). Since a careful reading of both texts revealed no obvious link between them (e.g. characteristic features of the medieval version that occur in *CupplesLeon* but not in the Perrault or Grimm tales from which it is certainly derived)) we assume this to be an estimation error (the precise cause of which would require a more detailed deconstruction of the search algorithm that is beyond the scope of the current paper). A more general problem with the interpretation of the results of the T-Rex analysis is that, like the parsimony and NeighbourNet structures, all the variants are represented as leaf nodes. Consequently, it is not easy to evaluate direct lines of descent between historical and modern variants, most particularly the relationships of Perrault and the Brothers Grimm to literary and oral tales that were published/recorded more recently.

Fig. 3 "T-Rex" about here.

4.3 PhyloDAG

We will now propose an alternative approach to network analysis. Our approach is likelihood based and, as we will show below, it solves many of the issues in existing network and tree-based methods.

Likelihood based phylogenetic inference involves a probabilistic sequence evolution model characterizing the evolutionary process. A popular example of such a model is the Jukes-Cantor model (Jukes & Cantor, 1969) that gives the probability of the four DNA symbols, A,T,G, and C, changing into other symbols or remaining unchanged in a certain period of time, and also depending on the mutation rate. Given such a model, the likelihood of a phylogenetic tree is obtained as the probability that the observed data sequences are produced when the tree structure is fixed and the lineages evolve independently according to the sequence evolution model and branching occurs according to the tree structure. The maximum likelihood method for phylogenetic inference attempts to find the tree structure, including the edge lengths that determine the expected amount of change along each edge, for which the likelihood is the highest possible.

Strimmer and Moulton (2000) describe a simple extension of the likelihood defined for phylogenetic trees that is also applicable to networks, hence allowing reticulation edges to be added into a tree. We improve and extend the method by Moulton and Strimmer in two ways. First, we introduce a more efficient technique for approximating the likelihood of phylogenetic network. Second, we propose a simple search procedure that considers additional reticulation edges in a given tree structure and also estimates the edge lengths by a simple sampling technique. As a result, our method which we call PhyloDAG operates in a similar fashion as T-Rex: it takes as input a matrix of character data such as DNA sequences or a set of features, and an initial tree structure, and produces a network where a given number of reticulation edges have been added to the tree, together with its likelihood value. In contrast to T-Rex, however, PhyloDAG can be used to evaluate tree and network structures where some of the extant taxa are placed at internal nodes so that they represent ancestors of some of the other taxa. For a more detailed description of the PhyloDAG method, see Appendix B. Different network or tree structures can be compared using a statistical test known as the parametric bootstrap, which we will also outline below, see Appendix C.

We start the PhyloDAG method with a parsimony tree, Fig. 1, obtained from data matrix in Table II. We then use PhyloDAG to evaluate its likelihood (setting the number of reticulation edges to zero). The parsimony tree yields log-likelihood the value –863.4. [2]

Next, we manipulated the topology of the tree to explore different scenarios concerning the origins of the literary and oral traditions of ATU 333. This involved moving the Perrault and Grimm texts into different internal positions in the tree where they would be either ancestral to both the oral and literary variants, or ancestral to the literary variants and collateral to the oral variants (i.e. descended from a common oral ancestor). We did not attempt manipulations which are incompatible with existing knowledge about the tales, such as the chronology of the literary variants (for example, we did not experiment with making Grimm's 1812 tale ancestral to Perrault's 1697 version). It is important to note that these manipulations alone will not, as a rule, yield a higher likelihood score than a normal tree. This is because any such manipulated tree is equivalent to a special case of a tree where the taxon in the internal position is in fact a leaf node but the edge pointing it has length zero. Hence, the likelihood value of the tree where the taxon is a leaf node will never be lower than the likelihood of the tree where it is an internal node when the edge lengths in both models are optimimized so as to maximize the likelihood. The interesting question is whether a hypothesis involving observed ancestral taxa is better when we allow possible contamination, i.e., reticulation edges in addition to the tree. The PhyloDAG method provides a tool for answering this question.

We used PhyloDAG to search for reticulation edges that improve the likelihood score. As a starting point for the search, we use different variations of the parsimony tree (Fig. 1) where either Perrault or Grimms is moved into an ancestral position, considering a number of different nearby positions just above or next to the position of the said taxa in the parsimony tree. The search produced 11 alternative structures, which we label by *a, b, c, d, e, f, g, h, i, j,* and *k*. Figures 5 and 6 show respectively networks *c* and *d*, which are of particular importance for our discussion below. The other networks are given for completeness in Appendix D.[3]

As an indication of how well the models "fit" the data, we report the log-likelihood value of each of the models. For example, the log-likelihood of network *c* is –862.4, and the log-likelihood of network *d* is –865.5. Networks *b, c* and g achieve a higher log-likelihood value than the parsimony tree (–863.4). However, the likelihood values should not be taken to be the final evaluation of the models because of two reasons. First, the likelihood evaluation is approximate due to the random sampling procedure included in the method (see Appendix B). Second, perhaps more importantly, the log-likelihood score tends to favor complex models because they have more adjustable parameters that make it easier to achieve high log-likelihood values for most data sets. To provide a statistically sound goodness-of-fit measure, below we propose to use a parametric bootstrap technique.

4. 4 Parametric Bootstrap

It is important to note that a network hypothesis is typically more complex than a tree hypothesis (it has more parameters), which may lead to so called over-fitting: choosing a too complex hypothesis considering its statistical support. To avoid over-fitting, we applied a parametric bootstrap test to compare the tree hypotheses and the different network hypotheses; for more details, see Appendix C.

Table I summarizes the results of the bootstrap test. The results are not unanimous but there is a relatively strong (considering the small sample size) signal indicating that models *b*, *c*, and *g* have the best statistical support. Among them, model *c* (fourth row in Table I, and Fig. 4) fares especially well, and is only rejected with low statistical confidence when compared to models *b* and *g*, while the latter two are both rejected in more comparisons. All three models place *Perrault* in an internal position that makes it ancestral to all the literary variants. However, there is some disagreement regarding the position of the Grimms' tale: Model *b* (see Appendix D) has *Grimm* as a terminal node, whereas both *c* and *g* place *Grimm* as an ancestral source for subsequent literary versions. Although the bootstrap test was unable to discriminate between these possibilities, previous research into the history of Little Red Riding Hood strongly support the latter scenario (Zipes, 1993).

TABLE I. STATISTICAL HYPOTHESIS TEST RESULTS (PARAMETRIC BOOTSTRAP). ROWS: NULL HYPOTHESIS. COLUMNS: ALTERNATIVE HYPOTHESIS. 'tree': PARSIMONY TREE. '·': NOT REJECTED. '+': REJECTED AT SIGNIFICANCE LEVEL 0.05. '*': REJECTED AT SIGNIFICANCE LEVEL 0.01.

NULL HYPOTHESIS	ALTERNATIVE HYPOTHESIS											
	tree	*a*	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*i*	*j*	*k*
tree		*	*	*	*	+	*	*	*	.	*	.
a	.		*	*	*	*	*	*	*	.	*	*
b	.	.		+	+	+	+	+	+	.	*	+
c	.	.	+		.	.	.	+	.	.	.	.
d	.	+	*	*		+	.	*	.	.	*	+
e	+	*	*	+	*		*	*	+	.	*	*
f	+	*	*	*	.	*		*	+	.	+	.
g	+	.	+	.	*	*	*		.	.	+	.
h	*	*	*	*	*	*	*	*		*	*	*
i	*	*	*	*	*	*	*	*	*		*	*
j	*	*	*	*	*	*	*	*	.	.		*
k	*	*	*	*	*	*	*	*	.	.	*	

Fig. 4 "PhyloDAG network c" about here.

More significantly, all three models *b, c*, and *g* are consistent with the oral origins hypothesis. The literary tradition instigated by Perrault (placed as an internal node in all three models) is represented as an offshoot of a lineage that also gave rise to the French and Italian tale 'The Story of Grandmother'. The models further suggest that the variants of the Italian tale of *Catterinetta* comprise a separate group that split from the other oral and literary variants prior to *Perrault*. However, the models show that these various subgroups of ATU 333 did not develop in isolation of one another. All three indicate contamination both within and between the literary and oral traditions of the tale. For example, like the T-Rex structure, models *b*, *c*, and *g*, all suggest reticulation played an important role in the tale *ThreeGirls*. However, whereas the T-Rex analysis suggested that *ThreeGirls* was descended from an oral ancestor that preceded the first written versions of Little Red Riding Hood, the PhyloDAG models are more consistent with the parsimony results, which situated the tale within the literary group. Specifically, models *b, c,* and *g*, indicate that *ThreeGirls* is descended from the Grimm's text, which was mixed with elements from oral tradition (notably the Italian *Catterinetta* tale, as shown in models *c* and *g*, with which it shares distinctive motifs like angering the villain by replacing the contents of the basket). Contamination also appears to be evident in the Portuguese tale *Consigliere* and French literary tale *Goldenhood*, which might explain their anomalous positions in the parsimony tree, which made them a sister clade to the Perrauldian literary tradition. As explained earlier, reticulation can be a major source of error in inferring phylogenetic trees, for example by dragging affected taxa deeper into the structure of the tree. By incorporating reticulation edges in PhyloDAG, we found that models in which Perrault was ancestral to *Consigliere* and *Goldenhood* fitted the data much better than models in which these tales formed a sister clade, i.e. *a* and *e*, which were rejected in all the bootstrap comparisons with every other model except one (*i*, discussed below).

We analysed six structures that supported the alternative literary origins hypothesis. Among them, the one that is best supported by the data – albeit not as well as the oral origins models, *b, c,* and *g* – is model *d,* see Fig. 5. The other network structures are given in Appendix D. Models *f*, *i* and *k* represent Perrault as the ancestor of all modern versions of ATU 333, including the literary variants and the oral tales 'The Story of Grandmother' and 'Catterinetta'. Model *f* represents the Grimm tale as a leaf node, while in *i* and *k* the Grimm tale is shifted into different internal positions within the PhyloDAG. In the bootstrap comparisons, all three models are rejected against the tree and the oral origin scenarios represented in *b*, *c* and *g*. Models *d*, *h* and *j* represent Perrault as the ancestor of the literary variants of Little Red Riding Hood and the oral tale 'The Story of Grandmother', but not of versions of 'Catterinetta', which consistently come out as a sister group to the other tales in the analyses. The Grimm tale is positioned as a leaf node in model *d* and as an internal node in *h* and *j*. Model *d* is supported against the parsimony tree, but rejected with high statistical support against the oral origins models *b*, *c*, and *g*. Models *h* and *j* are rejected in all the comparisons.

Fig. 5 "PhyloDAG network d" about here.

In sum, the inclusion of lineal and reticulate relationships using PhyloDAG produced a number of structures that fit the data better than the parsimony tree. Structures consistent with the oral origins hypothesis were less frequently rejected in the bootstrap comparisons than those that are consistent with the literary origins hypothesis, with all three of the top performing models (*b, c* and *g*) falling into the former category. However, it should be noted that the evidence from the bootstrap test comparisons is not all in one direction, since models *b* and *g* (oral) are rejected against *d* and *f* (literary). On the other hand, model *c* (oral) is supported with high statistical confidence against both literary origins models. Thus, overall, the results of the PhyloDAG analyses indicate that the literary tradition of Little Red Riding Hood has its roots in oral folktales, rather than the other way around.

5. Conclusions

Our aim in this paper has been to shed light on a complex question in the historiography of fairy tales: is it possible to identify whether particular stories originated as traditional folktales or authored texts? We have proposed that a useful strategy for addressing this question is to adopt the kind of quantitative, computational approach that has been so successfully used to reconstruct manuscript stemmata. Our case study focused on testing two long-standing competing hypotheses about the origins of Little Red Riding Hood. The first suggests the tale originally evolved in French and Italian oral tradition, adapted by Charles

Perrault in the late seventeenth century, and subsequently copied by The Brothers Grimm to establish the classic form of the tale found in present day popular culture. The second hypothesis proposes that the tale was a literary invention in the first place, and that "traditional" variants collected by folklorists are actually adaptations of Perrault's and Grimm's texts.

We initially tested these hypotheses by analysing 23 oral and literary variants of Little Red Riding Hood/ATU 333 using one the most popular methods in computer-assisted stemmatology – maximum parsimony analysis. While the general structure of the tree returned by this analysis seemed to be more compatible with the oral origins hypothesis than the literary origins hypothesis, this conclusion is mitigated by two problems with interpreting the results: firstly, maximum parsimony does not incorporate reticulation (contamination), which can lead to errors in estimating phylogenetic relationships; secondly, the method does not model lineal (ancestor-descendent) relationships among observed taxa, making it difficult to draw firm conclusions about the role of classic historic texts (i.e. Perrault and Grimm) on contemporary literary and oral variants. Alternative methods for modelling reticulate evolution, such as NeighbourNet and T-Rex, provide a means for addressing the first of these problems but not the second. As such, their usefulness for addressing the question in hand turned out to be limited. We therefore introduced a new approach – PhyloDAG – which handles both lineal and reticulate relationships in a statistically sound way. This enabled us to compare different models for the evolution of Little Red Riding Hood and directly test the oral hypothesis against the literary hypothesis. Our results pointed strongly toward the former, with the best models indicating that Perrault adapted his tale from oral folktales, rather than vice versa.

Of course, we cannot extrapolate any general conclusions about the origins of fairy tales from a single case study. It is entirely possible – likely, even – that other tales originated in a literary medium before passing into oral tradition, as suggested by Bottigheimer. What we have shown here is that the problem of establishing these facts is far from intractable, and can be solved using principled and powerful computational methods. We anticipate that the application of these methods will generate new insights into the origins and development of different types of fairy tale, as well as other kinds of cultural traditions (Lipo, O'Brien, Collard, & Shennan, 2006; Mace, Holden, & Shennan, 2005).

Endnotes

1 The SplitsTree4 software is available at www.splitstree.org .
2 We follow the convention to give likelihood values in logarithmic scale, so that probabilities, which are always less than one, become negative numbers.
3 We chose to include all 11 networks in order to give an indication of the range of possible network hypotheses we considered and to quantify the statistical uncertainty by means of the bootstrap test.

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Figures

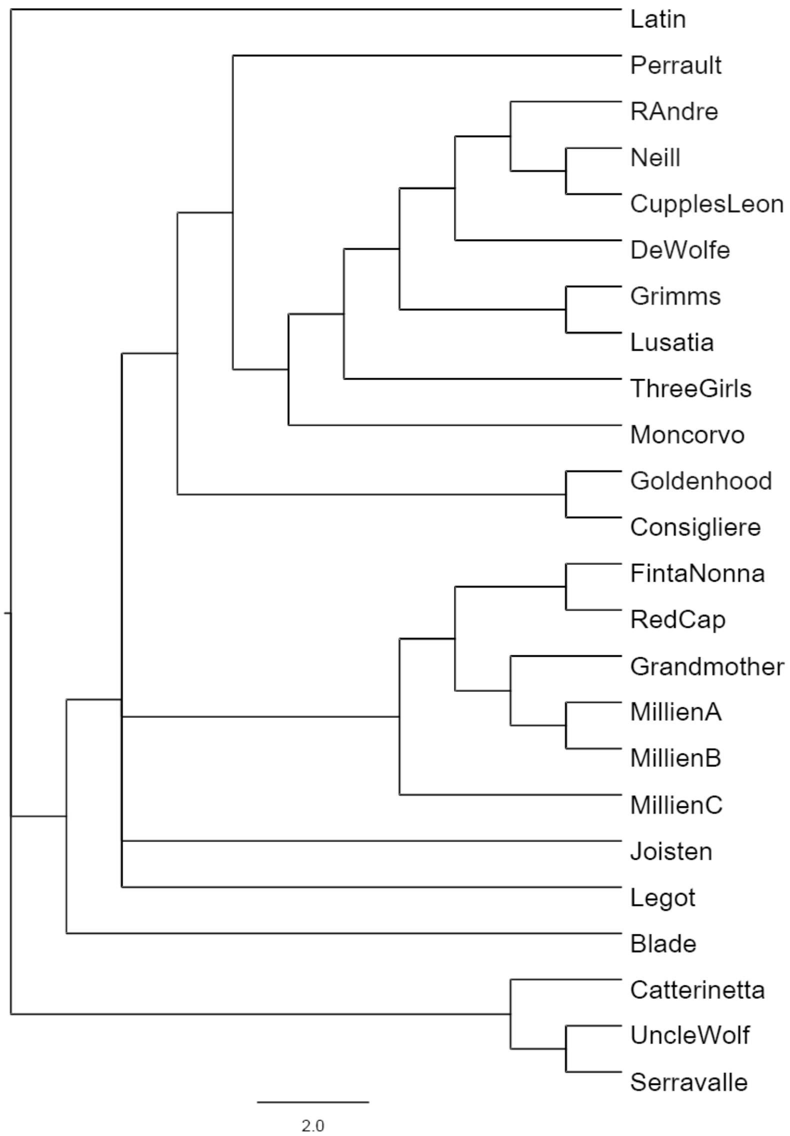


Fig. 1 Parsimony tree. Log-likelihood –863.4.

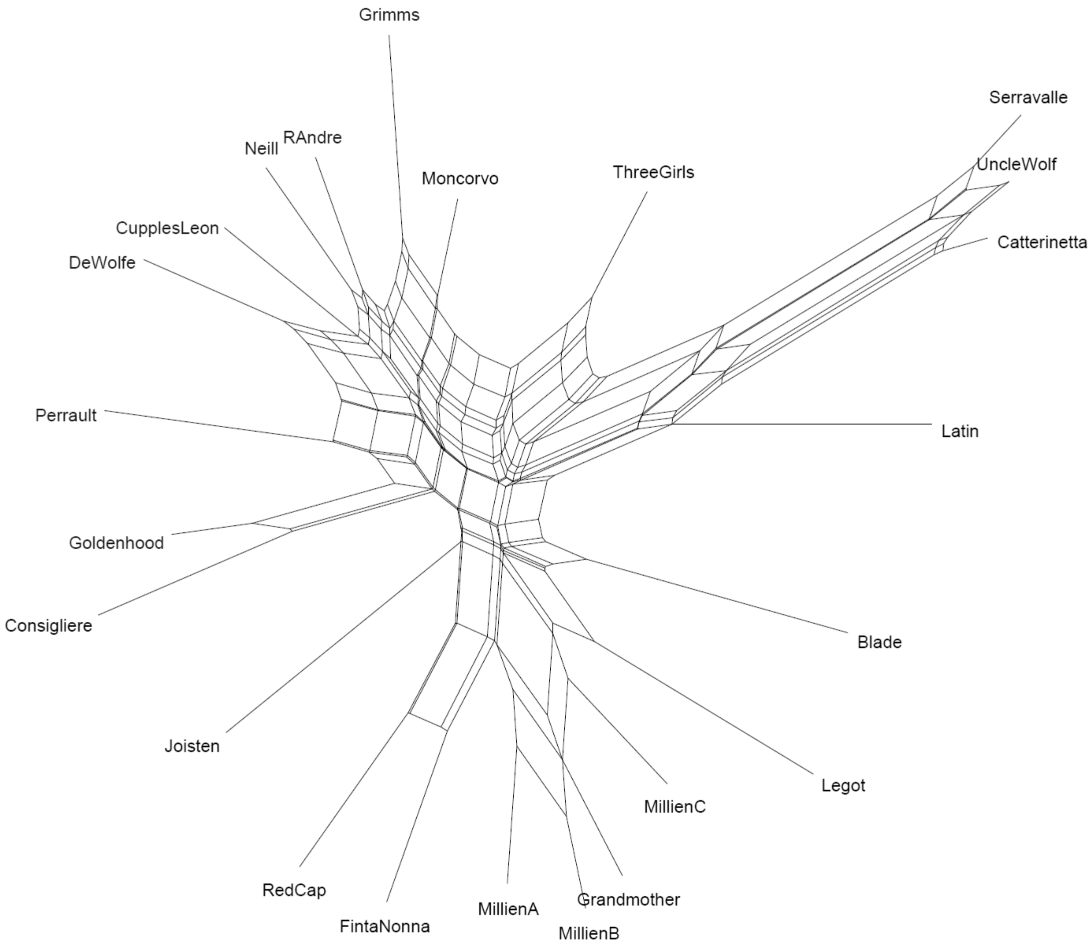


Fig. 2 NeighborNet. The network is obtained by Splitstree4 (Huson and Bryant, 2006) with default settings.

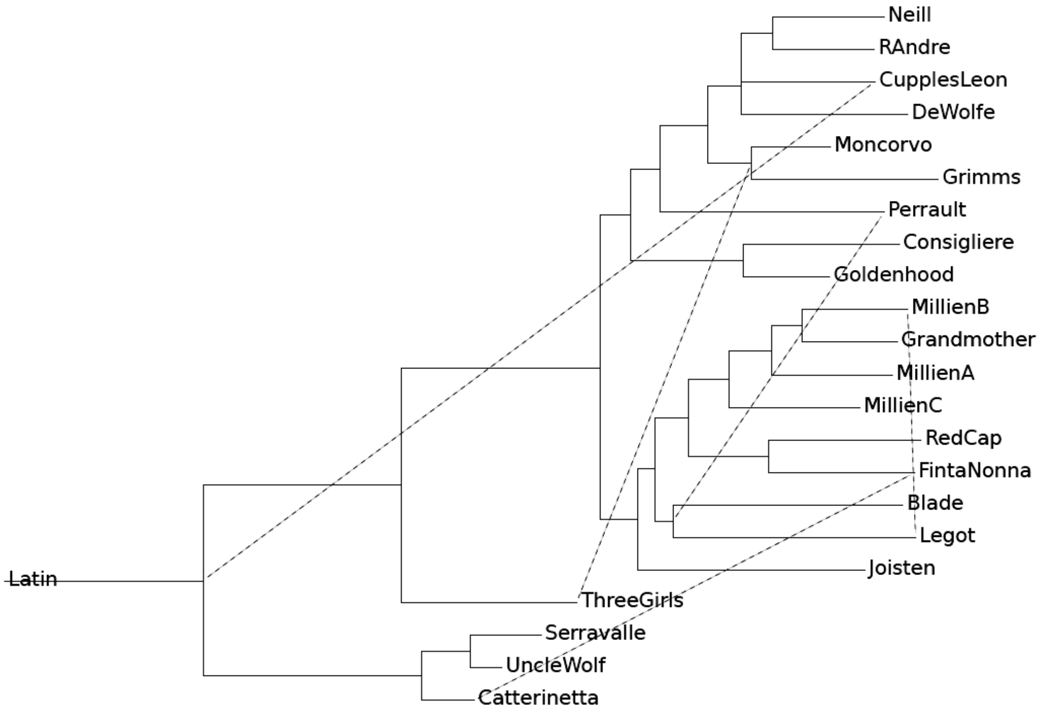


Fig. 3 T-Rex. The underlying Neighbor-Joining tree is shown with solid black lines and five additional reticulation edges are shown with dotted red lines.

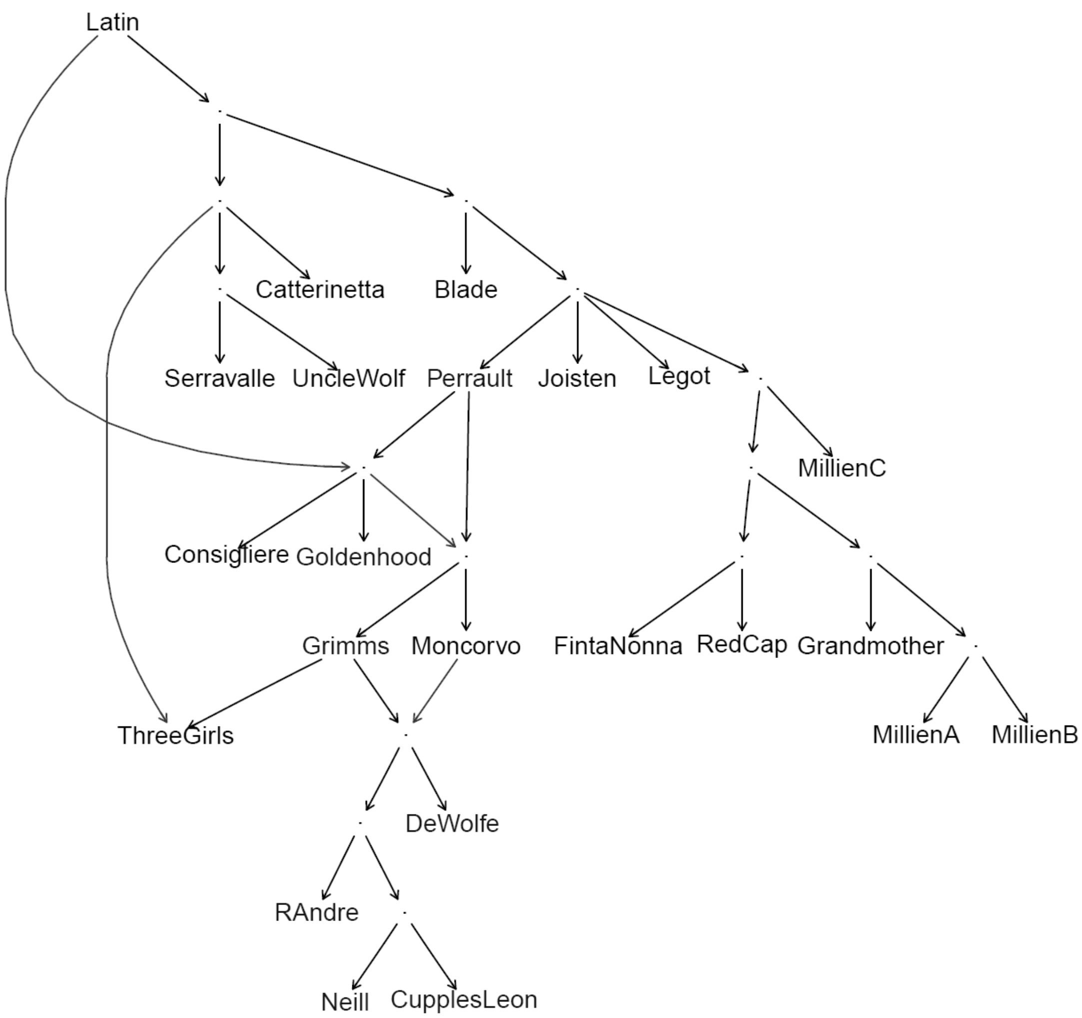


Fig. 4 PhyloDAG network *c*. Log-likelihood –862.4.

Fig. 5 PhyloDAG network *d*. Log-likelihood –865.5.

Appendix A. Data

Sources

Taxon name	Reference
Perrault	Perrault, C. (1697). "Le Petit Chaperon Rouge" *Histoire ou contes du temps passe.*
Grimm	Grimm J. & Grimm W. (1812). "Rotkäppchen". *Kinder- und Hausmärchen*. Gottingen, no. 26
Lusatia	A. H. Wratislaw (1889) "Little Red Hood". Sixty Folk-Tales from Exclusively Slavonic Sources London: Elliot Stock, pp. 97-100
Neill	Neill, J. (1908). *Little Red Riding Hood.* Chicago: Reilly & Lee Co. Downloaded from The University of Southern Mississippi Little Red Riding Hood Project: http://www.usm.edu/media/english/fairytales/lrrh/lrrhhome.htm
Randre	Andre, R. (1888). *Red Riding Hood.* New York: McLoughlin Bros. Downloaded from The University of Southern Mississippi Little Red Riding Hood Project: http://www.usm.edu/media/english/fairytales/lrrh/lrrhhome.htm
CupplesLeon	Gruelle J. B. (1916). *All About Little Red Riding Hood.* New York: Cupples & Leon. Downloaded from The University of Southern Mississippi Little Red Riding Hood Project: http://www.usm.edu/media/english/fairytales/lrrh/lrrhhome.htm
DeWolf	DeWolfe (1890). *Red Riding Hood and Cinderella*. DeWolfe, Fiske, and Co. Downloaded from The University of Southern Mississippi Little Red Riding Hood Project: http://www.usm.edu/media/english/fairytales/lrrh/lrrhhome.htm
Goldenhood	Marelles, C. 1895. "The True Story of Little Goldenhood". *Andrew Lang, The Red Fairy Book, 5th edition.* London and New York: Longmans, Green, & Co. pp. 215-19
Consigliere	Vaz da Silva, F. (1995). Capuchinho vermelho em Portugal. Estudos de Literatura Oral 1, p. 38-58
Moncorvo	Vasconcellos, L. (n.d.) "O Chapelinho Encarnado". Translated by Sara Silva. Courtesy of Isabel Cardigos and the Centro de Estudos Ataíde Oliveira
ThreeGirls	Calvino, I. (1956, trans. 1980 by G. Martin) "The Wolf and the Three Girls". *Italian Folktales.* Harmondsworth: Penguin, pp.26-27
MillenA	Millen, A. (1887). 'Little Red Riding Hood: Version 1'. Zipes, J. 2013. *The Golden Age of the Folk and Fairy Tales*. Indianapolis: Hackett. P 170-1

MillenB	Millen, A. (1887). 'Little Red Riding Hood: Version 2' zipes, J. 2013. *The Golden Age of the Folk and Fairy Tales*. Indianapolis: Hackett. P 172
MillenC	Millen, A. (1887). 'The Little Girl and the Wolf' zipes, J. 2013. *The Golden Age of the Folk and Fairy Tales*. Indianapolis: Hackett. P 173
Grandmother	Delarue, P. (1956). "The Story of Grandmother". *The Borzoi Book of French Folktales*. New York: Alfred Knopf, pp. 230-233.
FintaNonna	Calvino, I. (1956, trans. 1980 by G. Martin) "The False Grandmother". *Italian Folktales.* Harmondsworth: Penguin, pp.116-117
RedCap	Schneller, C. (1867, trans. 2007 by D. Ashliman). "Cappelin Rosso". *Märchen und Sagen aus Wälschtirol: Ein Beitrag zur deutschen Sagenkunde.*Innsbruck: Verlag der Wagner'schen Universitäts-Buchhandlung, pp. 9-10
Blade	Blade, Jean-Francois. (1886). 'The Wolf and the Child' zipes, J. 2013. *The Golden Age of the Folk and Fairy Tales.* Indianapolis: Hackett. P 169
Legot	Legot M. (1885). 'Little Red Riding Hood: The Version of Tourangelle'. Zipes, J. 2013. *The Golden Age of the Folk and Fairy Tales.* Indianapolis: Hackett. p167
Joisten	Joisten, C. Untitled. Recounted in Zipes, J. (1993) *The Trials and Tribulations of Little Red Riding Hood*. New York: Routledge, pp. 5-6.
Serravalle	Rumpf, M. (1958) "Caterinella: Ein italienisches Warnmärchen," Serravalle variant. ***Fabula*** 1: 76-84
UncleWolf	Calvino, I. (1956, trans. 1980 by G. Martin) "Uncle Wolf". *Italian Folktales.* Harmondsworth: Penguin, pp.49-50.
Catterinetta	Schneller, C. (1867, trans. 2007 by D. Ashliman). "Cattarinetta". *Märchen und Sagen aus Wälschtirol: Ein Beitrag zur deutschen Sagenkunde.*Innsbruck: Verlag der Wagner'schen Universitäts-Buchhandlung, pp. 8-9.
Latin	Ziolkowski, J. (1992) A fairy tale from before fairy tales: Egbert of Liege's "De puella a lupellis seruata" and the medieval background of "Little Red Riding Hood"

List of characters

1 Protagonist [0] girl [1] boy
2 Girl wears red hood: [0] absent [1] present
3 Who made red hood: [0] absent [1] mother [2] grandmother [3] godfather
4 Girl goes to visit relative: [0] absent [1] granny [2] aunt [3] mother
5 Relative is a witch: [0] absent [1] present [2] fairy]
6 Granny sick [0] absent [1] present
7 Girl told to fetch pan from relative: [0] absent [1] present

8 Girl told not to stay from path: [0] absent [1] present
9 Carries basket: [0] absent [1] present
10 Cargo: bread: [0] absent [1] present
11 Cargo: soup: [0] absent [1] present
12 Cargo: custard: [0] absent [1] present
13 Cargo: butter: [0] absent [1] present
14 Cargo: cakes: [0] absent [1] present
15 Cargo: eggs: [0] absent [1] present
16 Cargo: wine: [0] absent [1] present
17 Girl plays in forest: [0] absent [1] present
18 Girl eats the cargo: [0] absent [1] present
19 Villain is [0] ogre [1] wolf [2] werewolf [3] devil
20 Reconnaissance - villain finds out where the girl is going: [0] absent [1] present
21 Villain and girl take separate paths: [0] absent [1] pins vs needles [2] short vs long
22 Woodcutters are in the forest: [0] absent [1] present
23 Wolf impersonates girl: [0] absent [1] present
24 Grandmother gives instructions on opening door: [0] absent [1] present
25 Girl replaces cargo [0] absent [1] dung [2] nails
26 Monster eats granny: [0] absent [1] present
27 Monster dresses up in grannys clothes: [0] absent [1] present
28 Monster disguises voice: [0] absent [1] present
29 Girl eats remains of granny: [0] absent [1] present
30 Girl eats body parts: [0] absent [1] present [2] refuses
31 Girl eats granny teeth: [0] absent [1] present
32 Girl drinks blood: [0] absent [1] present [2] refuses
33 The girl is warned about the danger: [0] absent [1] by monster [2] by animals
34 Girl flees home boards up house: [0] absent [1] present
35 Monster stalks girl "I'm coming!": [0] absent [1] present
36 Wolf tells girl to take off clothes: [0] absent [1] present
37 Throws clothes into fire: [0] absent [1] present
38 Wolf tells girl to get into bed: [0] absent [1] present
39 Dialogue: [0] absent [1] present
40 My what! Head [0] absent [1] present
41 My what! Arms [0] absent [1] present
42 My what Feet [0] absent [1] present
43 My what! Legs [0] absent [1] present
44 My what! Ears [0] absent [1] present
45 My what! Teeth [0] absent [1] present
46 My what! Eyes [0] absent [1] present
47 My what! Nose [0] absent [1] present
48 My what! Hands [0] absent [1] present
49 My what! Mouth [0] absent [1] present
50 My what! Hairy [0] absent [1] present
51 Girl eaten: [0] absent [1] present
52 Girl cut out of stomach: [0] absent [1] present
53 Girl saved [0] absent] by [1] hunstman [2] woodcutters [3] father [4] mother [5] townsfolk [6] granny

54 Girl saved by magic cloak: [0] absent [1] present [2] magic wand

55 Girl tricks wolf: [0] absent [1] present

56 Wolf chases girl [0] no [1] to her house

57 Wolf killed: [0] absent [1] present

58 Wolf's stomach sewn up with stones inside

Matrix

[Character no.	**1 10 20 30 40 50]**
Latin	0130000009999999901000000000099900009009999999999909010000
Perrault	0121010010011000001121110111099900010110101110000010000000
RAndre	0111010010000001001120110111099900009010000111100009300010
DeWolfe	0121010010001110101121010011099900009010000111000009100010
Neill	0101000110001101101120010101099900009010000111100009300010
CupplesLeon	0111000010000000101101010001099900009010000110110009200010
Grimms	0121010110000101101120110110099900009010000101011011100011
Lusatia	0121010110000101101120110110099900009010000101011011100011
Goldenhood	0121000010000100001120000011099900010110100010001109610010
FintaNonna	0091001010000000000000000101111000010110001000011110001100
Grandmother	0091000010000000002110000101110120011110000000101109001100
Joisten	0101000010000100101110010100110110009011101010000109101110
RedCap	0101000010100000000110110101111110010110001100011110000000
Catterinetta	0092101010000100010000001000099900109009999999999910000000
UncleWolf	0092101010000101011000001000099901109009999999999910000000
Serravalle	0092101010000101011000001000099901109009999999999911400100
ThreeGirls	0093010010000101001110002100099900009011000000000011500010
Legot	0091010009999999003120000101100120009110101011000009001110
Blade	1092000009999999001100110110100100009110001011000110000000
MillienA	0091000011000000001111000100110120011110010101001110000000
MillienB	0091000011000000002111000100110120011110000011000009001100
MillienC	0091000011010000001110000100120200009110000110000109001100
Consigliere	0121200110000100002120100001000000009110101000001109620010
Moncorvo	01?1010010000100001120000101000000009110000101000011100011

N.B. the value 9 represents a “gap” state for characters that were redundant or not relevant for a particular tale. For example, if the girl did not carry a basket (character 9) then characters relating to the contents of the basket (10-16) – which logically could not be present – were coded as gap characters

Appendix B. Description of the PhyloDAG method

Strimmer and Moulton (2000) proposed a likelihood-based method for comparing different phylogenetic hypotheses that correspond to directed acyclic graphs (DAGs). Each node in the graph corresponds to a taxon, either extant or hypothetical (unobserved). The edges in the DAG correspond to direct inheritance where the origin of the edge, the "parent", is the immediate ancestor and the end of the edge, the "child", is the offspring. Cases where a taxon has only one parent are modelled by using familiar sequence evolution models such as the Jukes-Cantor model. However, when a taxon has more than one parent, a different evolutionary model is assumed: each of the parent taxa is given a relative weight, and each character is inherited from a parent that is randomly chosen based on these weights. Inheritance from a parent follows the same model as in the case where there is only one edge pointing to the node in question.

Computing the likelihood of a DAG model, i.e., the probability that a given set of sequences is obtained as the outcome of the given DAG, is hard. Moulton and Strimmer proposed a random sampling technique to approximate the likelihood. Their technique eventually converges to the exact likelihood value but in practice it may take a large number of samples, and hence, a long time, before obtaining accuracy that is sufficient for comparing different DAGs.

We have developed an alternative approximation which is not based on random sampling but instead uses a technique called loopy belief propagation, see (Murphy, Weiss, & Jordan, 1999). It is not guaranteed to converge to the exact value but on the other hand, it is often significantly faster than random sampling. In our experiments (not shown here, see (Nguyen & Roos, in preparation)), it produces better accuracy than a number of different random sampling techniques with less computation time. We also extend the earlier method by Strimmer and Moulton by including a parameter learning step where the edge lengths that characterize the amount of evolutionary change along each edge in the network are learned from the data so that they need not be given as input to the PhyloDAG method.

In practice, the PhyloDAG method takes as input a set of sequences and a tree structure. It then considers all possible additional edges between any two nodes in the tree – including edges between two extant nodes, edges between an extant and an hypothetical node, and edges between two hypothetical nodes – in turn and evaluates the likelihood of the network where the edge in question is included in addition to the edges in the initial tree structure. The edge or the edges that improve the likelihood score the most are included in the output network. Often it is useful to also set an upper bound on the number of edges that are added so as to obtain a more easily interpreted network where only the most significant reticulation events are included. In the present work, we limited the number of additional edges to four to facilitate the interpretation of the models.

We used the Jukes-Cantor model, which can be directly extended to handle any other number of character states than four, for modeling the evolution of individual features and following Moulton and Strimmer, set the weigths on the parents to be uniform so that each parent taxon has the same influence on the dependent taxon.

Appendix C. Parametric bootstrap

Parametric bootstrapping for testing phylogenetic topologies, i.e., tree structures, was first suggested by (Huelsenbeck & Crandall, 1997). Our implementation is primary based on the later description by (Posada, 2003). The testing procedure of topology M_0 (null hypothesis) against topology M_1 (alternative hypothesis) can be briefly described as follows.

1. Estimate the parameters (edge lengths) in models M_1 and M_0 by maximum likelihood. Denote the maximum likelihood estimates (MLEs) by θ_1 and θ_0, respectively.
2. Calculate the log-likelihood ratio (LLR) $l(D|\mathrm{M}_1, \theta_1) - l(D|\mathrm{M}_0, \theta_0)$, where $l(D|\mathrm{M}_1, \theta_1)$ and $l(D|\mathrm{M}_0, \theta_0)$ are the log-likelihood of the data given structure M_1 and M_0 with MLE parameters respectively.
3. From structure M_0 with estimated parameters θ_0, draw K=1000 simulated data sets which all have the same size and missing data as the original data set.
4. For each simulated data set D_i, estimate parameters $\tilde{\theta}_1$ and $\tilde{\theta}_0$ for both structures, and calculate the LLR $l(D_i|\mathrm{M}_1, \tilde{\theta}_1) - l(D_i|\mathrm{M}_0, \tilde{\theta}_0)$. Use these to obtain an approximate distribution of the LLR between M_0 and M_1 under the null hypothesis M_0.
5. Let F be the number of time that the LLR on simulated datasets is bigger than the LLR on the original data in Step 2. If the quotient F/K (in this case K=1000) is smaller than a predefined threshold (0.05 or 0.01), the null hypothesis is rejected.

The intuition is that if the null hypothesis is true, then the simulated data sets in Step 4 are drawn from the same distribution as the observed data. This implies that the LLR based on the observed data, computed in Step 2, follows the same distribution as the LLR values for the simulated data in Step 4. Suppose now that the LLR for the observed data, which measures how much better model M_1 fits the obsered data than M_0, is higher than almost all of the simulated LLR values. By the above reasoning, this must be unlikely since the observed LLR value is supposed to be drawn from the same distribution as the simulated ones, and we are lead to reject the null hypothesis. It is obvious that such a test is valid in the sense that if the null hypothesis is true, it is unlikely to be rejected.

Appendix D. Additional results.

Networks *c* (Fig. 4) and *d* (Fig. 5) are representative examples among the two main hypotheses: the oral origins hypothesis (network *c*) and the literary origins hypothesis (network *d*). Figures 6–14 show the rest of the networks for completeness.

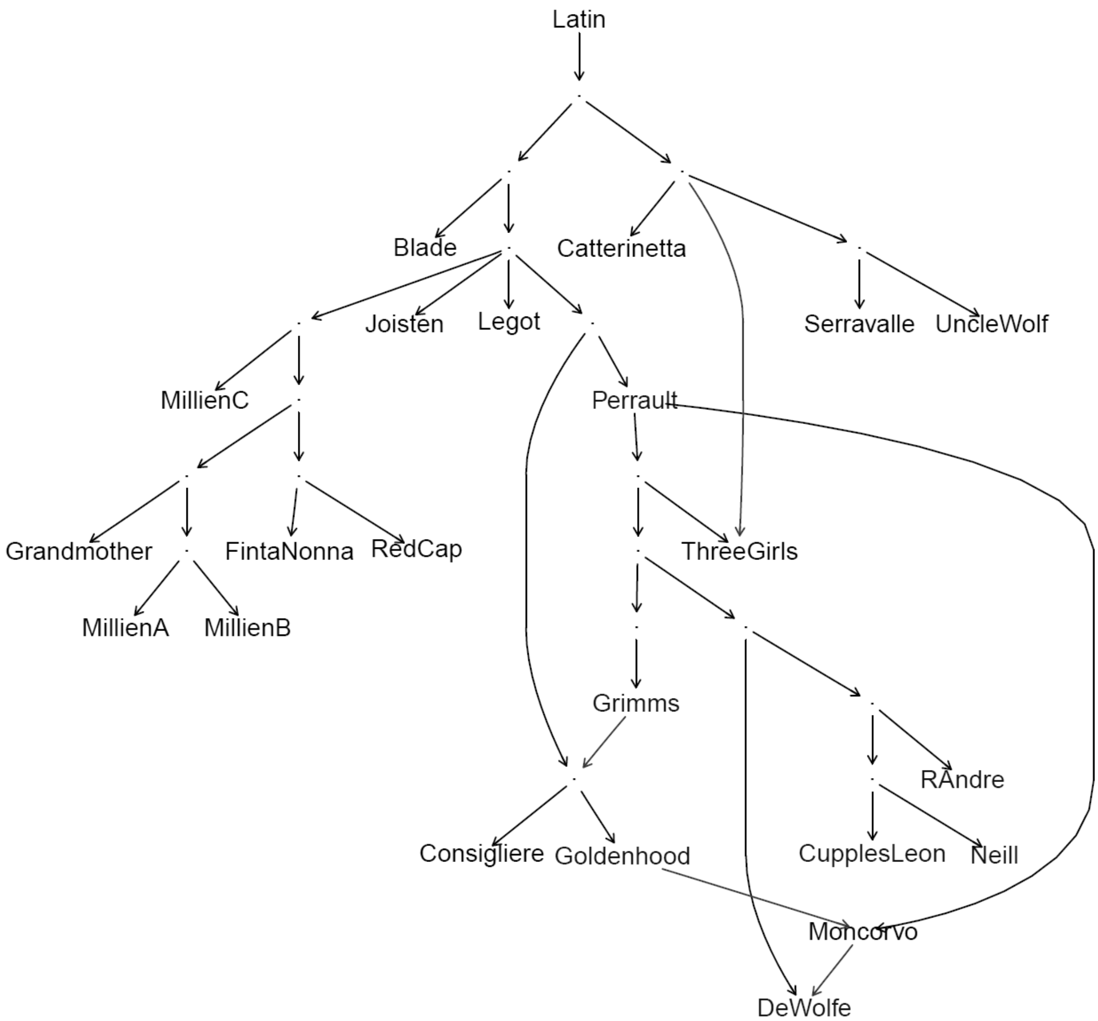


Fig. 6 PhyloDAG network *a*. Log-likelihood –875.6.

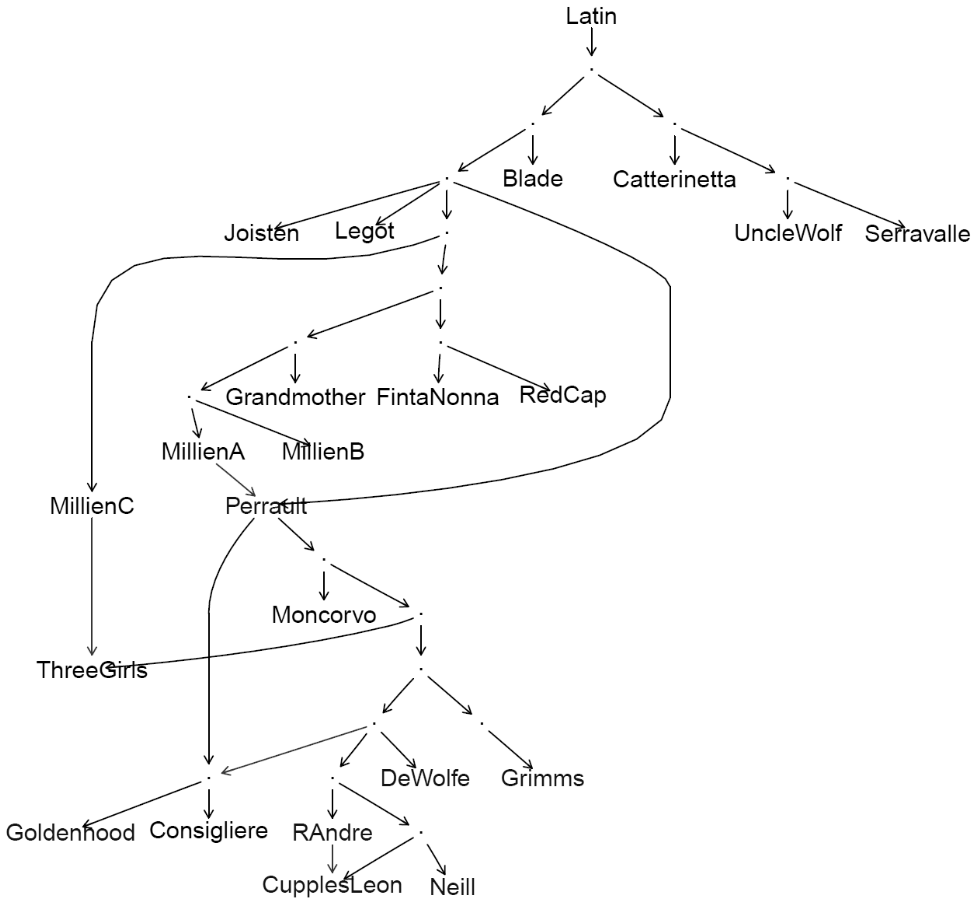


Fig. 7 PhyloDAG network *b*. Log-likelihood –862.3.

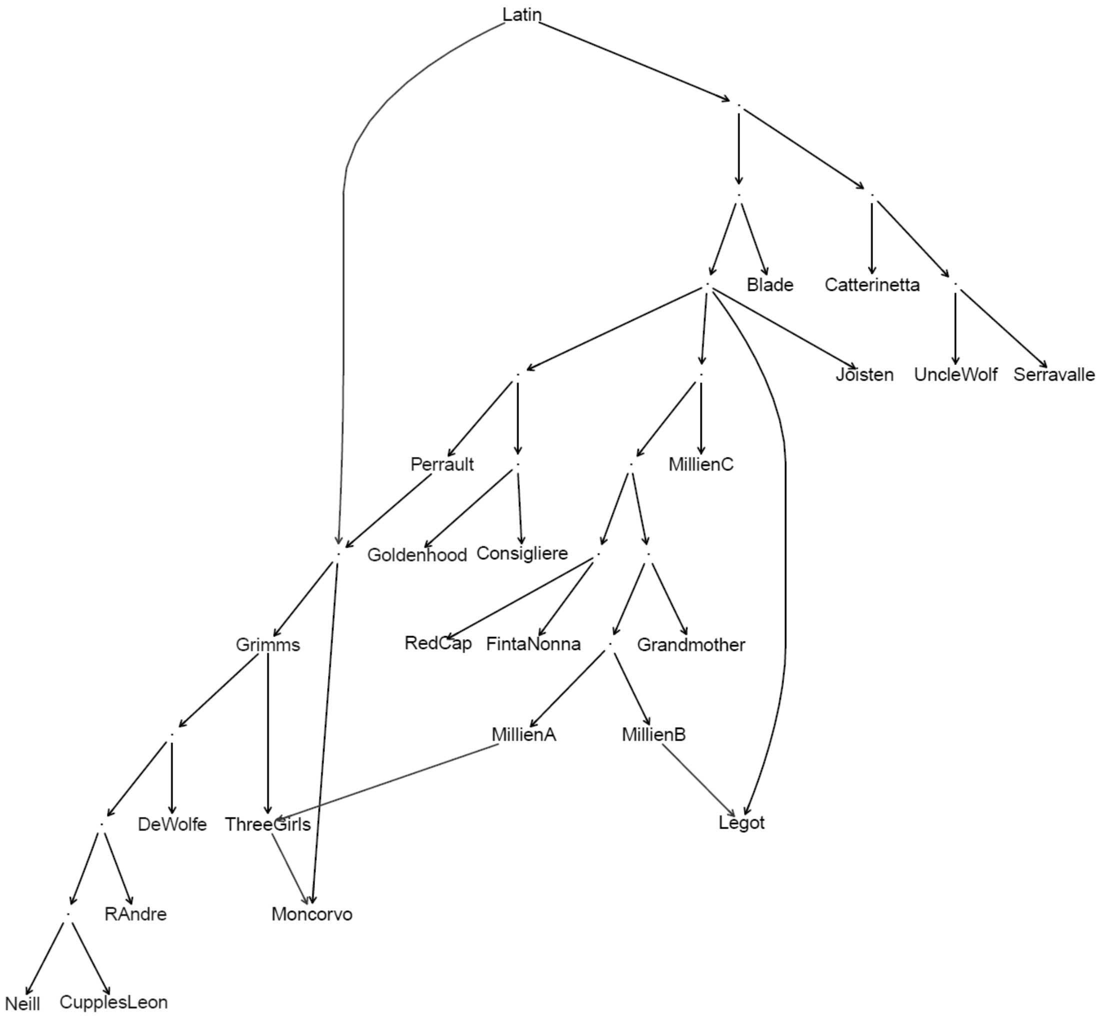
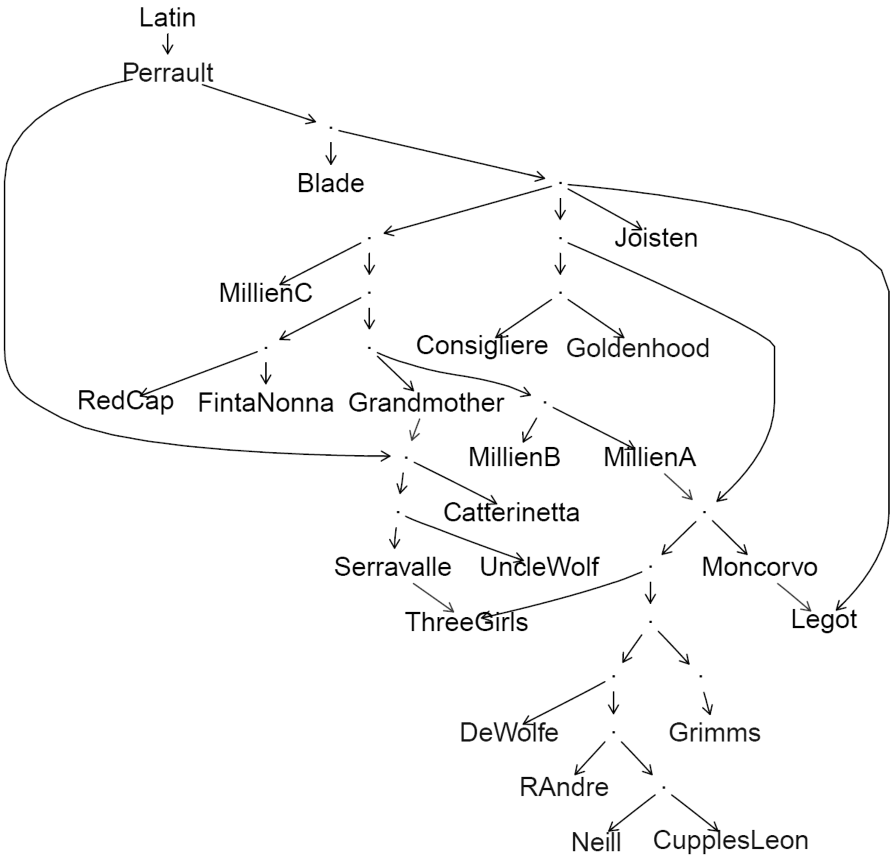


Fig. 8 PhyloDAG network *e*. Log-likelihood –867.0.



771
772 Fig. 9 PhyloDAG network *f*. Log-likelihood –884.6.
773

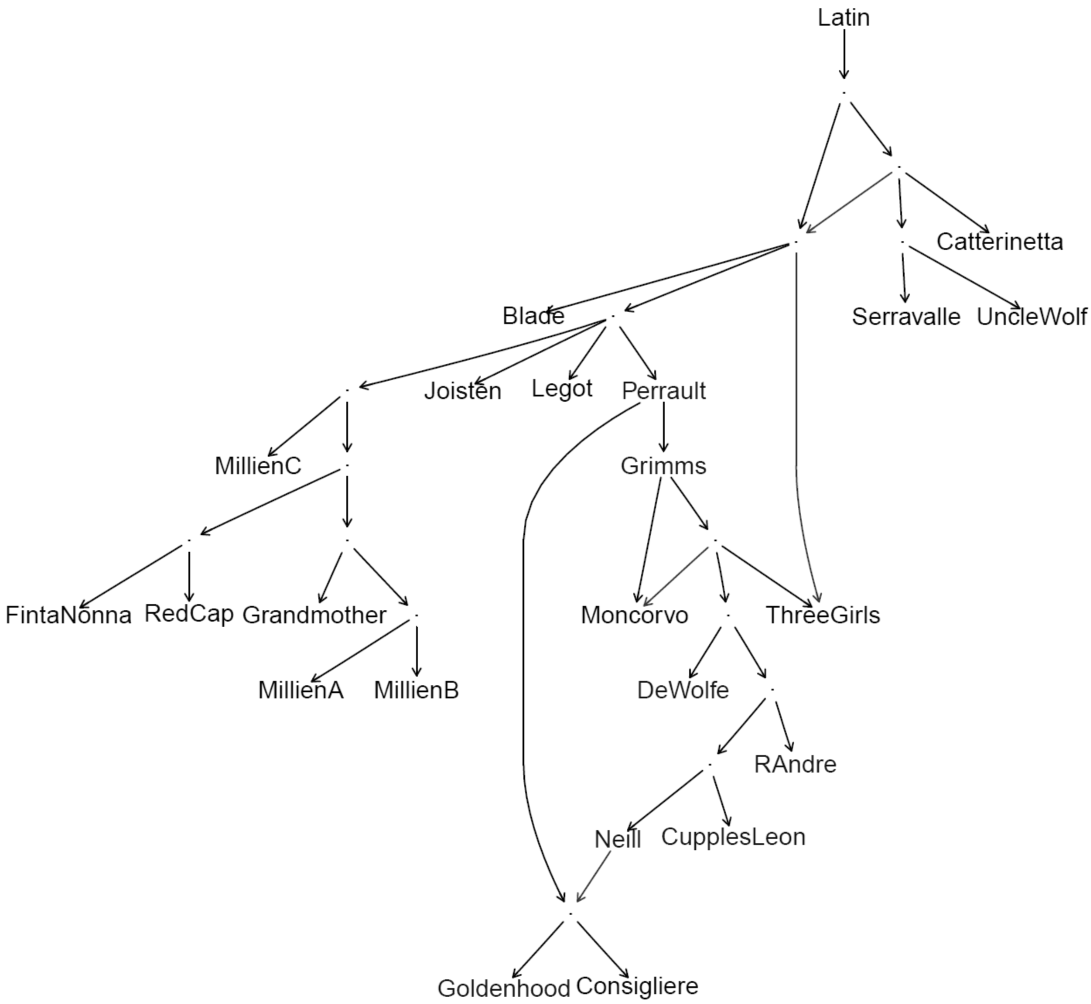


Fig. 10 PhyloDAG network *g*. Log-likelihood –847.6.

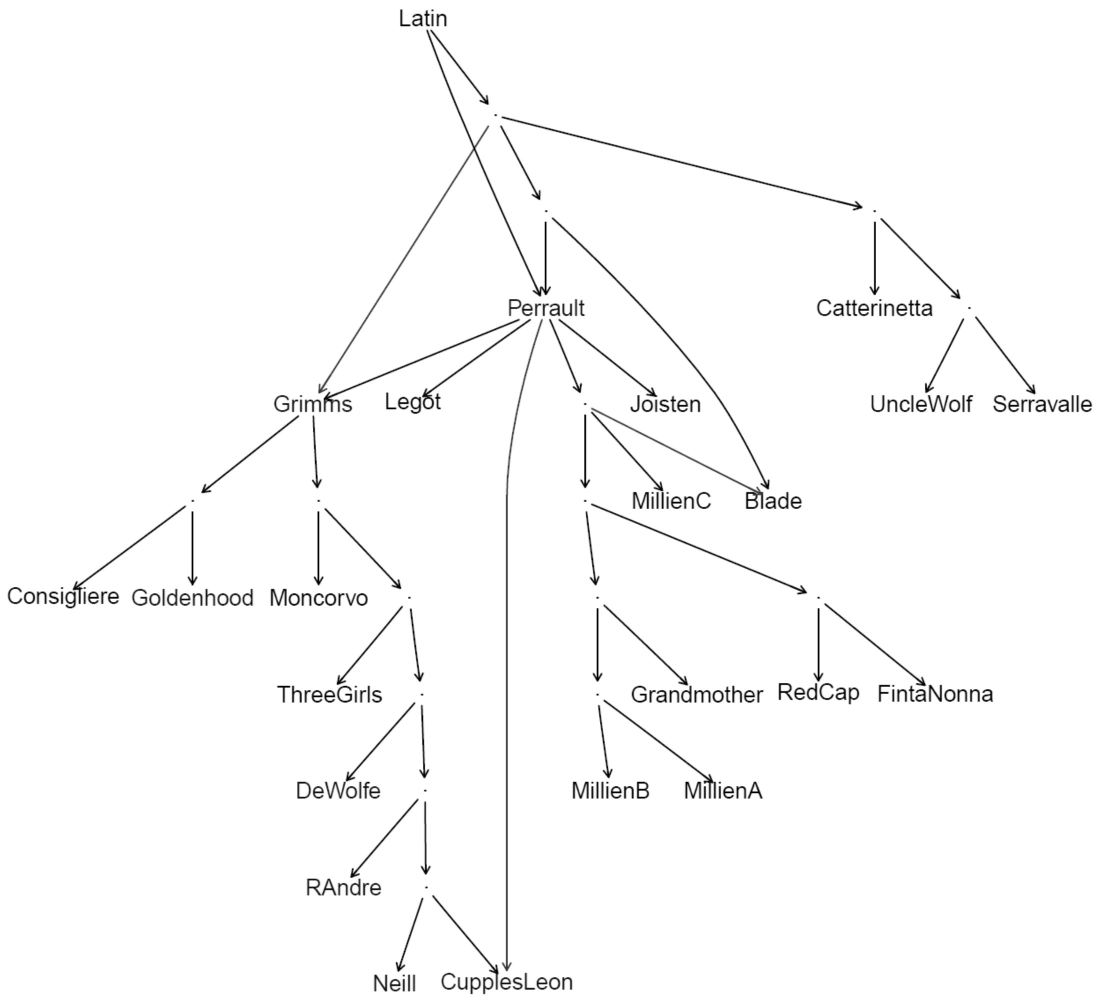


Fig. 11 PhyloDAG network *h*. Log-likelihood –896.76.

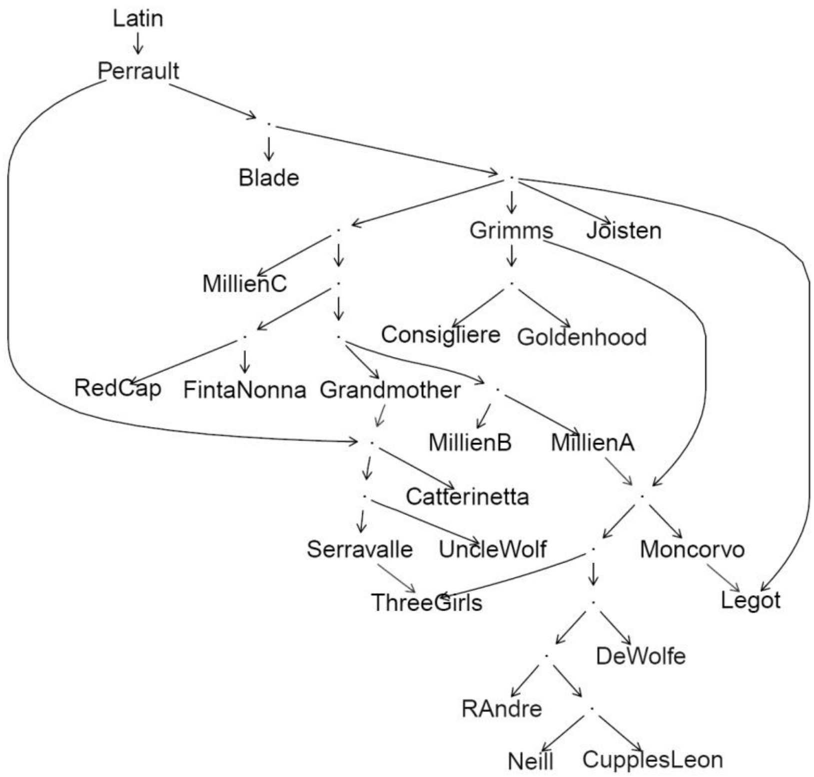


Fig. 12 PhyloDAG network *i*. Log-likelihood –897.32.

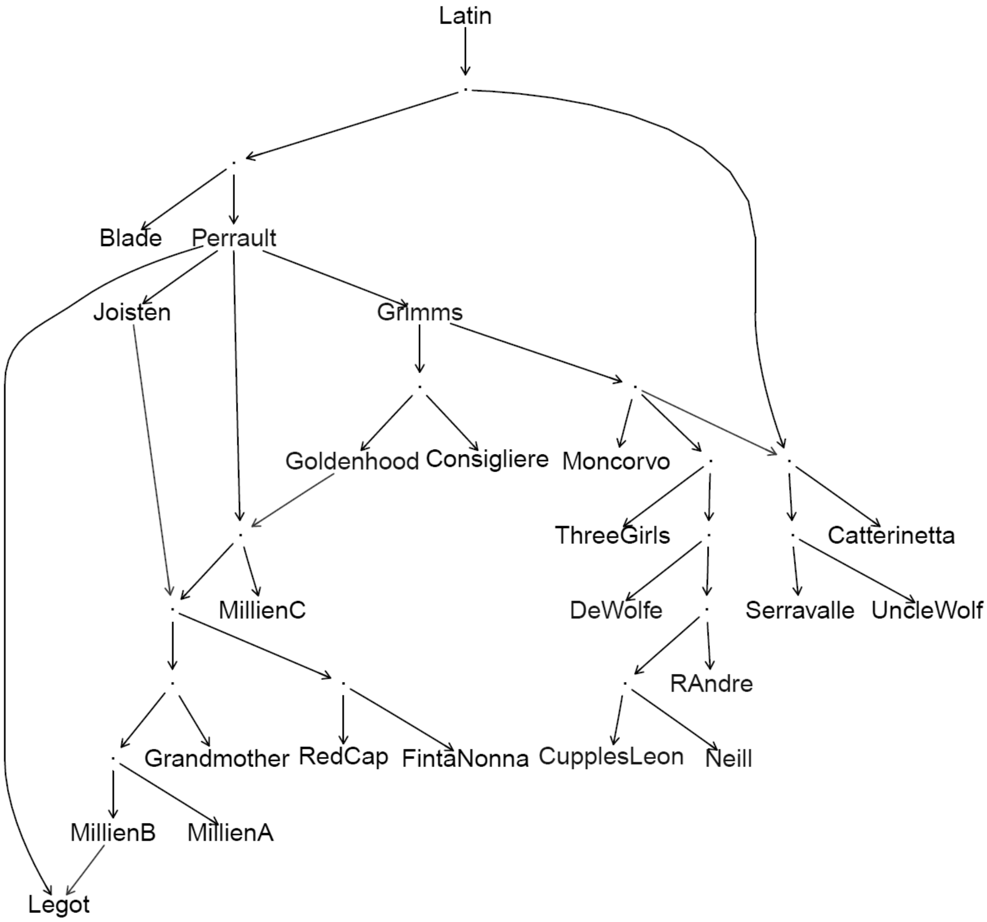


Fig. 13 PhyloDAG network *j*. Log-likelihood -870.13.

Fig. 14 PhyloDAG network *k*. Log-likelihood -870.87.