

## Phylogenetic analysis reveals a scattered distribution of autumn colours

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- **Background and Aims** Leaf colour in autumn is rarely considered informative for taxonomy, but there is now growing interest in the evolution of autumn colours and different hypotheses are debated. Research efforts are hindered by the lack of basic information: the phylogenetic distribution of autumn colours. It is not known when and how autumn colours evolved.
- **Methods** Data are reported on the autumn colours of 2368 tree species belonging to 400 genera of the temperate regions of the world, and an analysis is made of their phylogenetic relationships in order to reconstruct the evolutionary origin of red and yellow in autumn leaves.
- **Key Results** Red autumn colours are present in at least 290 species (70 genera), and evolved independently at least 25 times. Yellow is present independently from red in at least 378 species (97 genera) and evolved at least 28 times.
- **Conclusions** The phylogenetic reconstruction suggests that autumn colours have been acquired and lost many times during evolution. This scattered distribution could be explained by hypotheses involving some kind of coevolutionary interaction or by hypotheses that rely on the need for photoprotection.

**Key words:** Autumn colour, leaf colour, comparative analysis, coevolution, photoprotection, phylogenetic analysis.

### INTRODUCTION

#### *Autumn colours*

The colour change of leaves in autumn is a spectacular phenomenon, well known to everybody. It is also well known that not all tree species have autumn colours. However, the autumn colour of leaves is rarely listed among the characters for the identification of a species, in taxonomic keys, or in general in the botanical literature. I am not aware of any botanical text with ‘autumn leaf colour’ as a consistent systematic key for identifying a species. Fine details of the colours of flowers and even of mature (non-senescent) leaves are given, but autumn leaf colour seems to escape continuously the interest of taxonomists.

One possible explanation is that autumn colours are a transient phenomenon, but it is not rare for autumn colours to last for up to 2 months (e.g. Archetti and Leather, 2005). This is not a negligible amount of time, especially considering that some species, in some locations, may retain their leaves for only a few months per year. Another possible reason for this lack of interest is that autumn colours were thought to be, until not long ago, a by-product of leaf senescence, of no particular ecological or evolutionary meaning. This view is now considered incorrect (Archetti *et al.*, 2009).

Autumn colours are produced (Sanger, 1971; Matile, 2000; Lee and Gould, 2002) by two main classes of compound: carotenoids (yellow–orange) and anthocyanins (red–purple), although in some cases other pigments are used (for example 6-hydroxykynurenic acid for the brilliant yellow of *Ginkgo biloba*; Matile *et al.*, 1992). Whereas carotenoids are present

all year round and become visible during leaf senescence because of the degradation of chlorophyll (Biswal, 1995), anthocyanins are actively produced in autumn (Sanger, 1971; Lee, 2002; Lee and Gould, 2002). The reason for the production of anthocyanins in autumn is not yet clear (Ougham *et al.*, 2008), but it is clear that autumn colours are not simply a side-effect of leaf senescence (Archetti *et al.*, 2009).

#### *Hypotheses and comparative data*

There is now a growing interest in different hypotheses about the adaptive value of autumn colours (Archetti *et al.*, 2009; Ougham *et al.*, 2008). Adaptive explanations of autumn colours were already proposed a century ago (reviewed by Lee and Gould, 2002), suggesting that red pigments might help against the harmful effects of light at low temperature, but they were largely forgotten until a few years ago (Gould *et al.*, 1995; Feild *et al.*, 2001; Hoch *et al.*, 2001). A new different explanation suggests that autumn colours may be warning signals of high levels of chemical defences to insects (like aphids) that exploit the tree as a host in autumn (Archetti, 2000; Hamilton and Brown, 2001). These and other ideas are still debated (Archetti *et al.*, 2009; Ougham *et al.*, 2008). At least ten different hypotheses now exist (Archetti, 2009), and most of them remain untested.

Comparative studies have been hindered so far by the lack of basic information: the phylogenetic distribution of autumn colours. Hamilton and Brown (2001) had to derive the colours for their list of tree species from field guides. It seems that autumn colours are more interesting to amateurs than to professional botanists, which may explain why gardening books and field guides are the only texts that sometimes

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mention the autumn colours of different species (e.g. Little, 1980; Krussmann, 1985). In fact, there is no text with a comprehensive list of autumn colours by species. Lee *et al.* (2003) seems to have the longest list based on direct observations (89 species) available in the literature, but they report presence or absence of anthocyanins, which in some cases (if the amount is low) does not necessarily translate into presence of autumn colours. The 262 species listed by Hamilton and Brown (2001), on the other hand, were derived from field guides and contain some notable errors. For example, *Acer palmatum*, a popular ornamental species with many varieties cultivated for their bright autumn colours, is reported as green.

#### Rationale of this study

The first aim of this paper is to try and fill this gap by providing a list of the autumn colours of many hundreds of species growing in the temperate regions of the world. The task is huge, and it is not possible for the list to be exhaustive. It includes 2368 species belonging to 400 genera, growing in all the temperate regions of the world. This information would be relevant for systematics, even if it was irrelevant for ecology and evolution, but hopefully it will be used especially as a reference for comparative studies on the evolution of autumn colours.

The second aim is to study the phylogenetic history of autumn colours. It turns out that their distribution is broadly scattered: autumn colours have been acquired and lost independently many times during evolution. These results will be discussed in relation to the main hypotheses for the evolution of autumn colours.

## METHODS

#### Data source

The list includes 2368 species belonging to 400 genera (see Supplementary Data, available online). Most of these species are present at Westonbirt Arboretum, near Tetbury in Gloucestershire, UK, the most extensive tree collection in the UK, established in 1829 and managed by the UK Forestry Commission. It comprises some 18 000 trees belonging to about 3000 species. Other collections that I have used to compile the list are the Harcourt Arboretum of Oxford University (UK), the Arnold Arboretum of Harvard University, Massachusetts (USA), the Real Jardín Botánico, Madrid (Spain), the Royal Botanic Gardens, Kew (UK), the Brogdale National Fruit Tree Collection, Faversham (UK), and field sites in the UK, Italy, France, Norway, Chile, Argentina, Kyrgyzstan and Kazakhstan. The list provided in this paper is the result of data collection in different locations since 2000, although the final and most systematic survey was done in autumn 2007 at Westonbirt. Other sources used to double check the data are the *Manual of Cultivated Trees and Shrubs* (Kraussman, 1985), the list provided by Hamilton and Brown (2001), itself a summary of three field guides, and *Trees of Britain and Northern Europe* (White and Moore, 2003).

#### Colour classification

The classification is based on my categorization of the colours yellow, red and green, a categorization that would probably be similar for other (non-colour-blind) human observers. Although brown, orange and purple are also sometimes mentioned, these three categories can always be thought of as special cases of three basic colours: green, red and yellow. Orange can be considered intermediate between red and yellow, purple can be considered intermediate between red and green (Fig. 1) and brown is usually preceded by yellow, and the species are therefore classified as yellow in most cases.

False positives (species listed as red or yellow that are, in fact, green) are unlikely. Red and yellow are listed only when I was sure that the species consistently has red or yellow leaves in autumn, not restricted to a few individual leaves. False negatives (species listed as green that do have autumn colours), on the contrary, are possible especially for yellow, which in some cases is difficult to distinguish from light green. This survey was done sporadically over several years, but in autumn 2007 leaf colours were monitored at regular intervals (twice per week) from their inception until leaf fall. Some species were present as more than one individual at Westonbirt and some species were present in more than

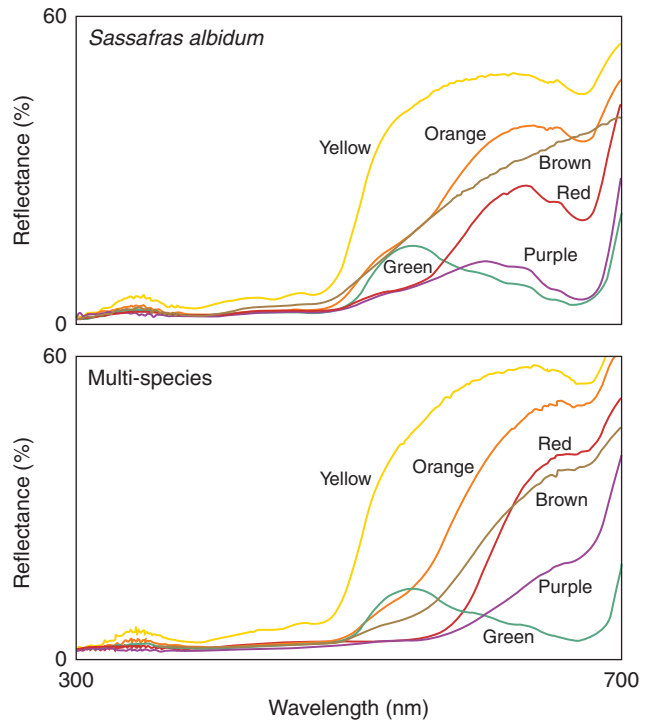


FIG. 1. Leaf colours. Average spectra of 100 leaves (21 green, 24 yellow, 10 orange, 28 red, 13 purple, 4 brown) collected on the same day from a single individual of *Sassafras albidum* and of 129 leaves (50 green, 28 yellow, 2 orange, 30 red, 24 purple, five brown) belonging to 21 different species (*Acer japonicum*, *Acer miyabei*, *Acer palmatum*, *Acer rubrum*, *Acer saccharum*, *Carya illinoensis*, *Fothergilla major*, *Parrotia persica*, *Phormium tenax*, *Prunus cerasifera*, *Prunus sargentii*, *Pseudolarix amabilis*, *Quercus ellipsoidalis*, *Quercus incana*, *Quercus palustris*, *Quercus rubra*, *Rhododendron luteum*, *Stewartia monadelphica*, *Stewartia ovata*, *Torreya californica*, *Typha latifolia*). Data and colour categories from Döring *et al.* (2009).

one collection. I double-checked with the available literature as described above. All this should reduce the number of false negatives, but they are still possible.

Only a few cases of conflicting reports occurred. When other authors (Kraussman, 1985; Hamilton and Brown, 2001; White and Moore, 2003) did not report autumn colours for a species but I observed personally and consistently autumn colours for that species, I assumed that it was a false negative in their records and my observations prevail. There are only a few cases in which the contrary occurred, i.e. I did not observe autumn colours but other authors mention autumn colours for that species. When I was sure about the other source (namely, when at least two authors independently mention the presence of autumn colours) I assumed I had recorded a false negative and corrected my data (only three such cases occurred). A few uncertain cases were discarded.

#### Phylogenetic trees

I used the phylogenetic trees in Soltis *et al.* (2007) for the angiosperms (see also Soltis *et al.*, 2005), and Brunsfeld *et al.* (1994) for the gymnosperms. These phylogenetic trees are resolved at the genus level. For the phylogenetic analysis, the standard parsimony reconstruction method of the software Mesquite (Maddison and Maddison, 2007) was used.

## RESULTS

The complete list of species with autumn colours is given in the Supplementary Data available online. In what follows, the number of red/yellow/green/total species is indicated for each genus. For example ‘*Acer*, 42/50/29/85’ means that within the 85 species included for the genus *Acer*, 29 are green, 42 red and 50 yellow. Note that most red species are also yellow, therefore the number of red, yellow and green species does not sum up to the total number of species. Green means that neither yellow nor red is present in autumn. Figures 2–8 report presence of red or yellow for each genus in a phylogenetic tree.

#### Non-core eudicots (Fig. 2)

Among non-core eudicots the species with red autumn colours belong to only five genera. *Sassafras* (1/1/0/1) represents an independent origin of red, as autumn colours are not present in any other member of Laurales and only once in another member of the magnoliids (*Magnolia*, 1/7/18/26). Within Ranunculales, *Euptelea* (2/2/0/2) represents an independent origin from the group including *Mahonia* (3/0/4/7) and *Berberis* (8/2/33/41). Yellow evolved independently in *Lindera* (0/5/1/6), *Liriodendron* (0/2/0/2), *Decaisnea* (0/1/0/1), *Platanus* (0/2/3/5) and *Meliosma* (0/1/1/2).

#### Core eudicots (excluding rosids and euasterids I and II; Fig. 3)

It is uncertain whether red evolved independently or was lost a number of times. Red is present in Cornales in *Nyssa*

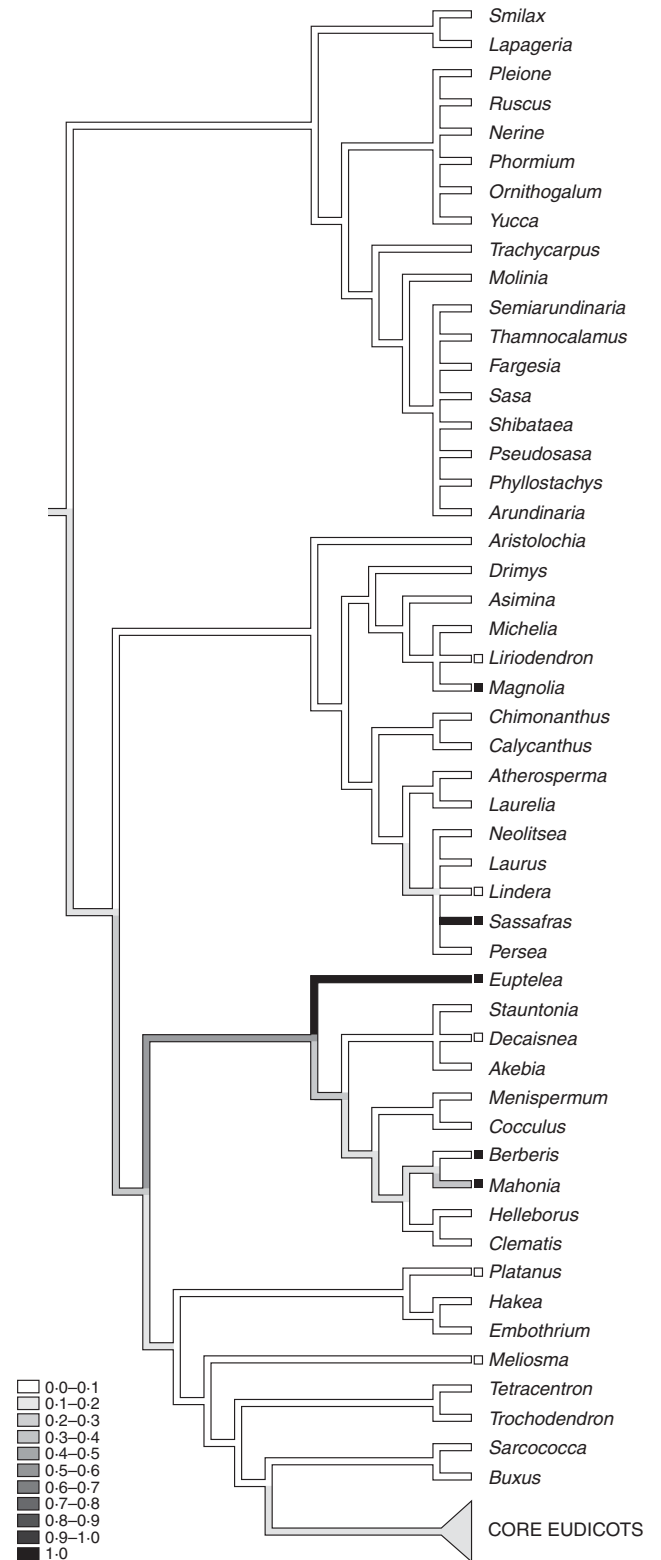


FIG. 2. Non-core eudicots. Presence of red (black squares) and yellow (white squares). Branches are coloured in greyscale proportional to the frequency of red species in that taxon.

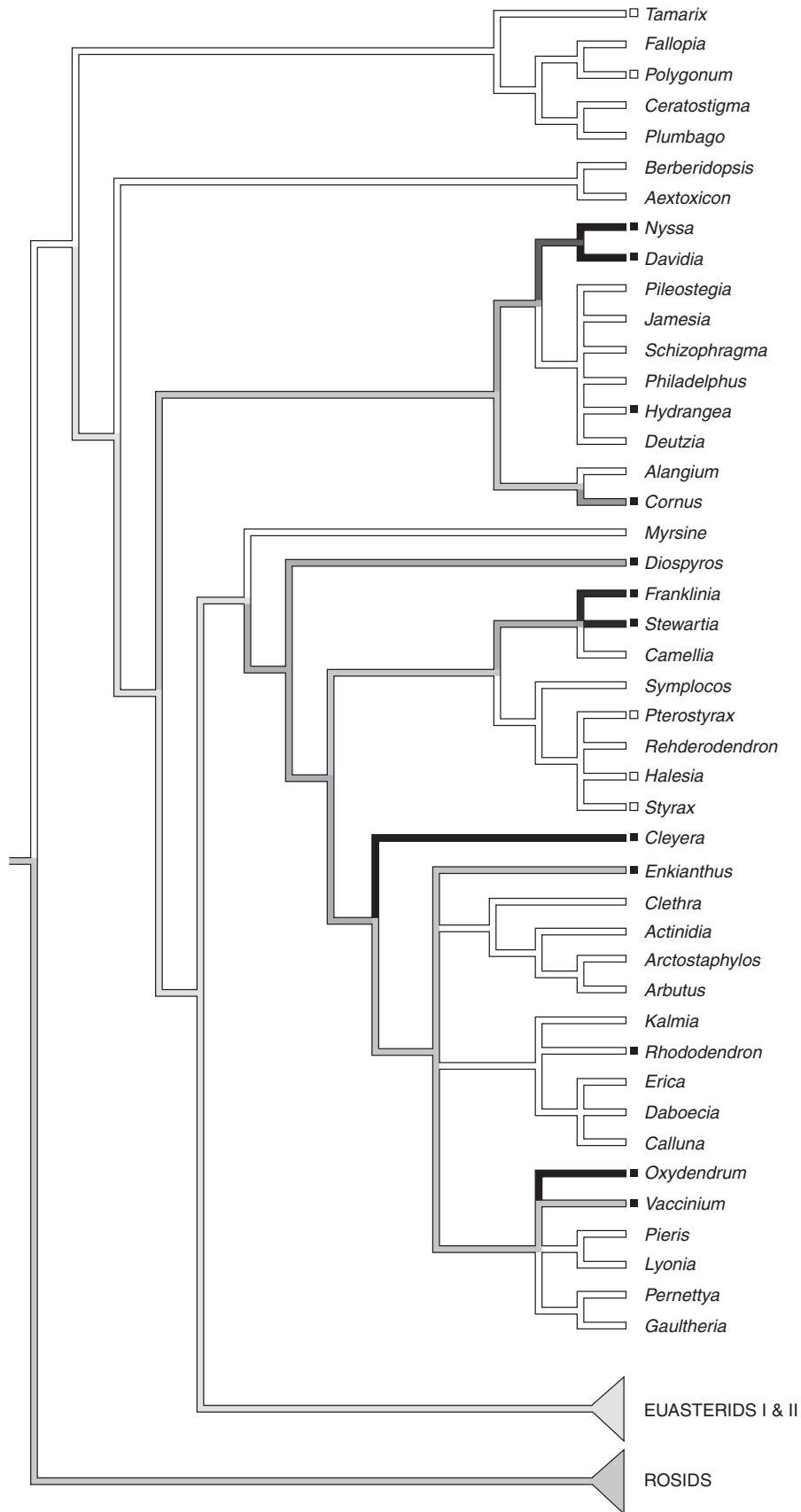


FIG. 3. Core eudicots. Other details as in Fig. 2.

(2/2/0/2), *Davidia* (1/1/0/1), *Hydrangea* (1/5/7/12) and *Cornus* (13/4/11/24). In Ericales, it is present in *Cleyera* (1/0/0/1), *Franklinia* (1/1/0/1), *Diospyros* (1/3/0/3), *Stewartia* (7/5/0/7), *Enkianthus* (1/2/3/5), *Oxydendrum* (1/0/0/1), *Vaccinium* (1/0/3/4), *Rhododendron* (6/3/120/127), *Halesia* (0/2/1/3), *Pterostyrax* (0/1/3/4) and *Styrax* (0/2/2/4) (all *Styracaceae*), and *Polygonum* (0/1/0/1) and *Tamarix* (0/1/1/2) have only yellow autumn colours.

#### *Euasterids I and II* (Fig. 4)

Red evolved once in *Dipsacales* (*Weigela*, 1/2/6/8; *Symphoricarpos*, 1/0/2/3; *Viburnum*, 9/0/31/40; *Heptacodium*, 1/0/0/1; *Kolkwitzia*, 1/1/0/1). At least two other independent origins occurred in *Fraxinus* (2/11/21/33) and *Forsythia* (1/0/3/4). *Aralia* (0/1/7/8), *Ilex* (0/1/40/41), *Lonicera* (0/2/31/33) and three other species in *Lamiales* have only yellow autumn colours: *Catalpa* (0/1/5/6), *Callicarpa* (0/1/5/6) and *Chionanthus* (0/1/0/1).

#### *Rosids* (excluding *eurosids I*; Fig. 5)

Evolution of red may have occurred independently at least five times. Alternatively, red must have been lost many times during evolution to account for its scattered distribution in this group. Red is present in *Crossosomatales* (*Stachyurus*, 2/1/2/4), *Myrtales* (*Lagerstroemia*, 1/1/0/1) and *Vitaceae* (*Vitis*, 1/0/4/5). In *Sapindales* red is present in *Rutaceae* (*Orixa*, 1/0/0/1, *Picrasma* 1/1/0/1), *Anacardiaceae* (*Rhus*, 9/0/3/12; *Cotinus* 2/2/0/2) and *Sapindaceae* (*Aesculus*, 6/8/2/12; *Koelreuteria*, 1/1/1/2; *Acer*, 43/49/29/86). In *Saxifragales*, it is present in *Cercidiphyllum* (2/2/0/2), *Ribes* (1/2/13/16), *Liquidambar* (4/1/0/4), *Parrotia* (1/1/0/1), *Fothergilla* (1/1/0/1), *Disanthus* (1/1/0/1), *Sinowilsonia* (1/1/0/1) and *Hamamelis* (2/4/2/6). Genera with yellow only are *Tilia* (0/11/10/21), *Staphylea* (0/1/6/7), *Phellodendron* (0/1/2/3), *Zanthoxylum* (0/2/5/7) and *Parrotiopsis* (0/1/0/1).

#### *Eurosids I* (Fig. 6; excluding *Rosales* and *Fabales* – see below)

Among *eurosids I*, autumn colours are present especially in *Rosales* and *Fagales* (see below) but also in *Celastrales* (at least two independent origins in *Eucryphia*, 1/1/3/4 and *Euonymus*, 11/8/13/24) and in *Malpighiales*, where it evolved independently at least twice in *Hypericum* (2/2/9/11) and *Poliothyrsis* (1/0/0/1). Yellow only is present in *Cercis* (0/2/3/5), *Cladrastis* (0/1/1/2), *Gleditsia* (0/3/3/6), *Robinia* (0/1/6/7) (all *Fabaceae*), in *Populus* (0/8/15/23) and in *Salix* (0/2/124/126).

#### *Rosales* and *Fabales* (Fig. 7)

Red in *Rosales* evolved independently at least twice: once in *Cannabaceae* (*Zelkova*, 2/2/4/6) and at least once in *Rosaceae* (*Stephanandra*, 2/2/0/2; *Holodiscus*, 1/0/1/1; *Rubus*, 1/0/7/8; *Prunus*, 20/12/51/74; *Aronia*, 3/1/0/3; *Mespilus*, 1/1/0/1; *Cydonia*, 1/0/0/1; *Cotoneaster*, 6/5/33/38; *Sorbus*, 24/25/53/91; *Photinia*, 3/2/4/7; *Crataegus*, 6/8/33/44; *Amelanchier*, 5/5/5/10; *Pyrus*, 6/1/11/18; *Malus*, 10/12/19/34). In *Fagales*, red evolved at least five times: in *Nothofagus* (13/13/25/38;

note that some *Nothofagus* species become red in winter before leaf fall, which may happen every second year; these species are included in the count), *Quercus* (17/21/60/90), *Carpinus* (2/3/10/14), *Betula* (2/20/22/42), *Corylus* (1/4/5/9). Yellow (at least seven independent origins) is the only autumn colour in *Fagus* (0/6/1/7), *Castanea* (0/3/1/4), *Carya* (0/6/4/10), *Pterocarya* (0/1/5/6), *Juglans* (0/7/5/12), *Ostrya* (0/1/2/3), *Morus* (0/4/5/5), *Ulmus* (0/4/12/16), *Kerria* (0/1/0/1) and *Rhamnus* (0/3/5/8).

#### *Conifers* (Fig. 8)

Autumn colours are not restricted to angiosperms, as is commonly believed. Red/brown autumn colours evolved in *Taxodium* (2/0/0/2) and *Metasequoia* (1/0/0/1) and golden/yellow colours in *Larix* (0/6/6/12) and *Pseudolarix* (0/1/0/1). *Ginkgo* (0/1/0/1) is also yellow and represents a clearly independent origin.

## DISCUSSION

In summary, red autumn colours are present in at least 290 species (70 genera), and evolved independently at least 25 times: once in the gymnosperms, four times in non-core eudicots and the remaining 20 in the core eudicots (including 16 times in the rosids). Yellow (the breakdown of chlorophyll that allows carotenoids to stand out in autumn, without concomitant production of red anthocyanins) is present in at least 378 species (97 genera), and evolved independently at least 28 times: twice in the gymnosperms, five in non-core eudicots and the remaining 21 in the core eudicots (including 15 times in the rosids). These are all conservative estimates. This scattered distribution is somewhat unexpected, and suggests that autumn colours have appeared and been lost many times during evolution.

It is perhaps surprising that the majority of species do not change colour in the autumn. Red leaves are present in only 12.1 % of the species considered (or 13.5 % if the gymnosperms are excluded) and yellow leaves in only 15.8 % of the species considered (or 17.6 % if the gymnosperms are excluded). Even excluding evergreen angiosperms these values do not change much. Autumn colours, therefore, are not the norm in deciduous species and it should not be taken for granted that they are a normal side-effect of leaf senescence.

#### *Relevance for the hypotheses on the evolution of autumn colours*

Explaining the interspecific distribution is one of the main problems for a consolidated explanation of autumn colours (Archetti *et al.*, 2009). This problem is even more pressing in the light of the present results. What is the reason of this scattered distribution?

If autumn colours are warning signals against parasites (Archetti, 2000; Hamilton and Brown, 2001), red or yellow leaves would be expected to be found only in species that have coevolved with parasites, and their scattered distribution would not be surprising, because host–parasite coevolution is usually species-specific, and not all species have parasites in autumn. Hamilton and Brown (2001) found that the presence

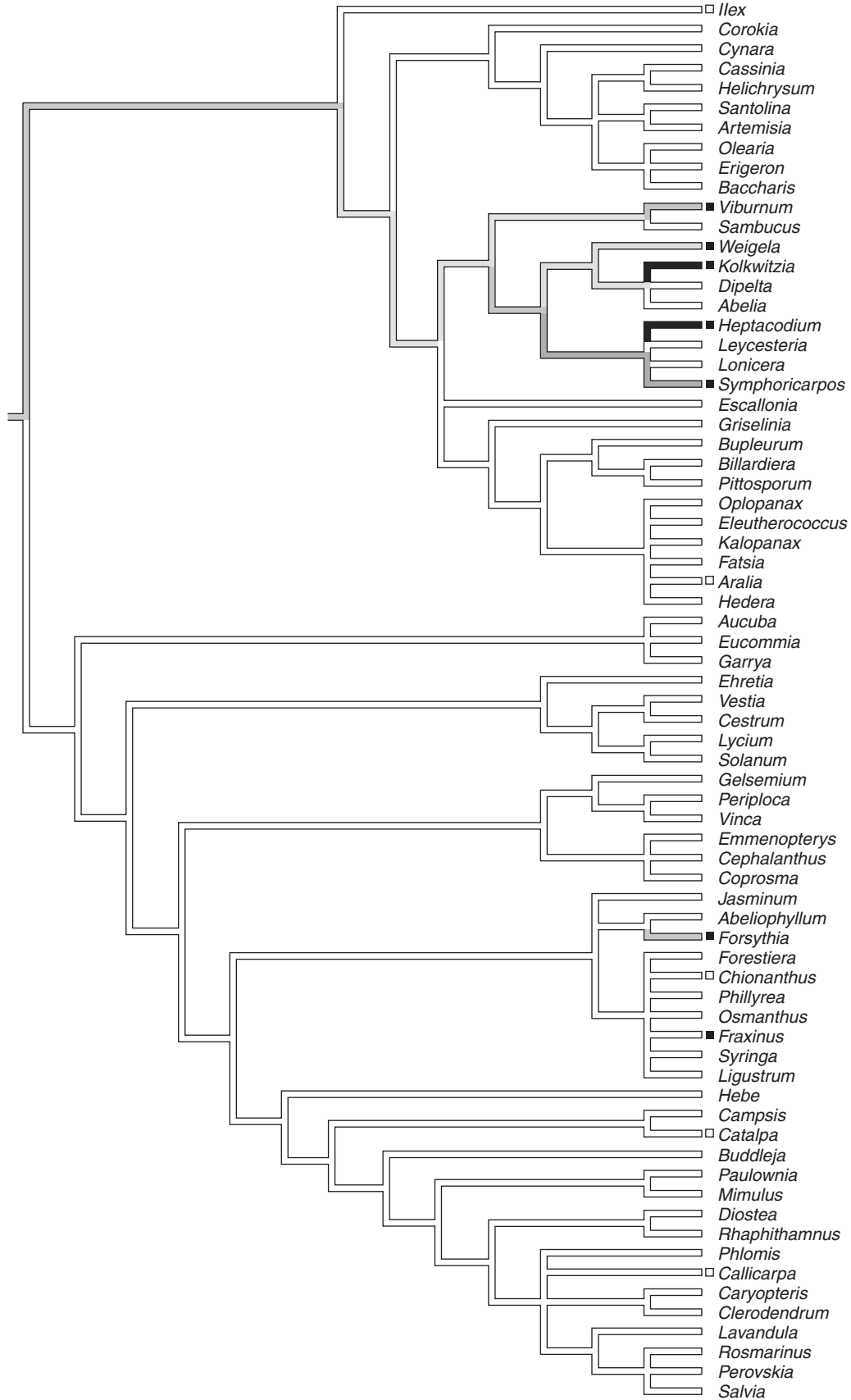


FIG. 4. Euasterids I and II. Other details as in Fig. 2.

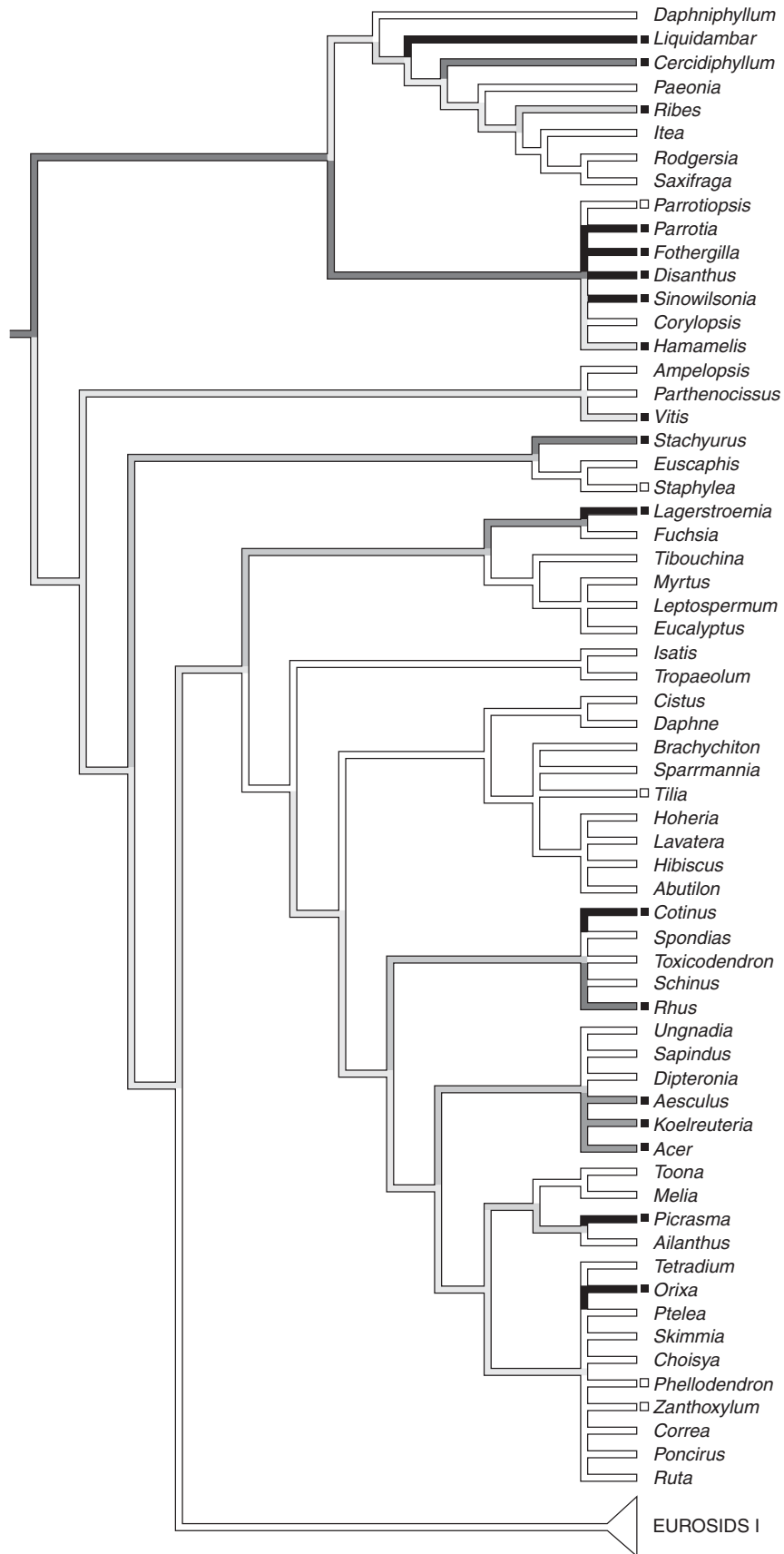


FIG. 5. Rosids. Other details as in Fig. 2.

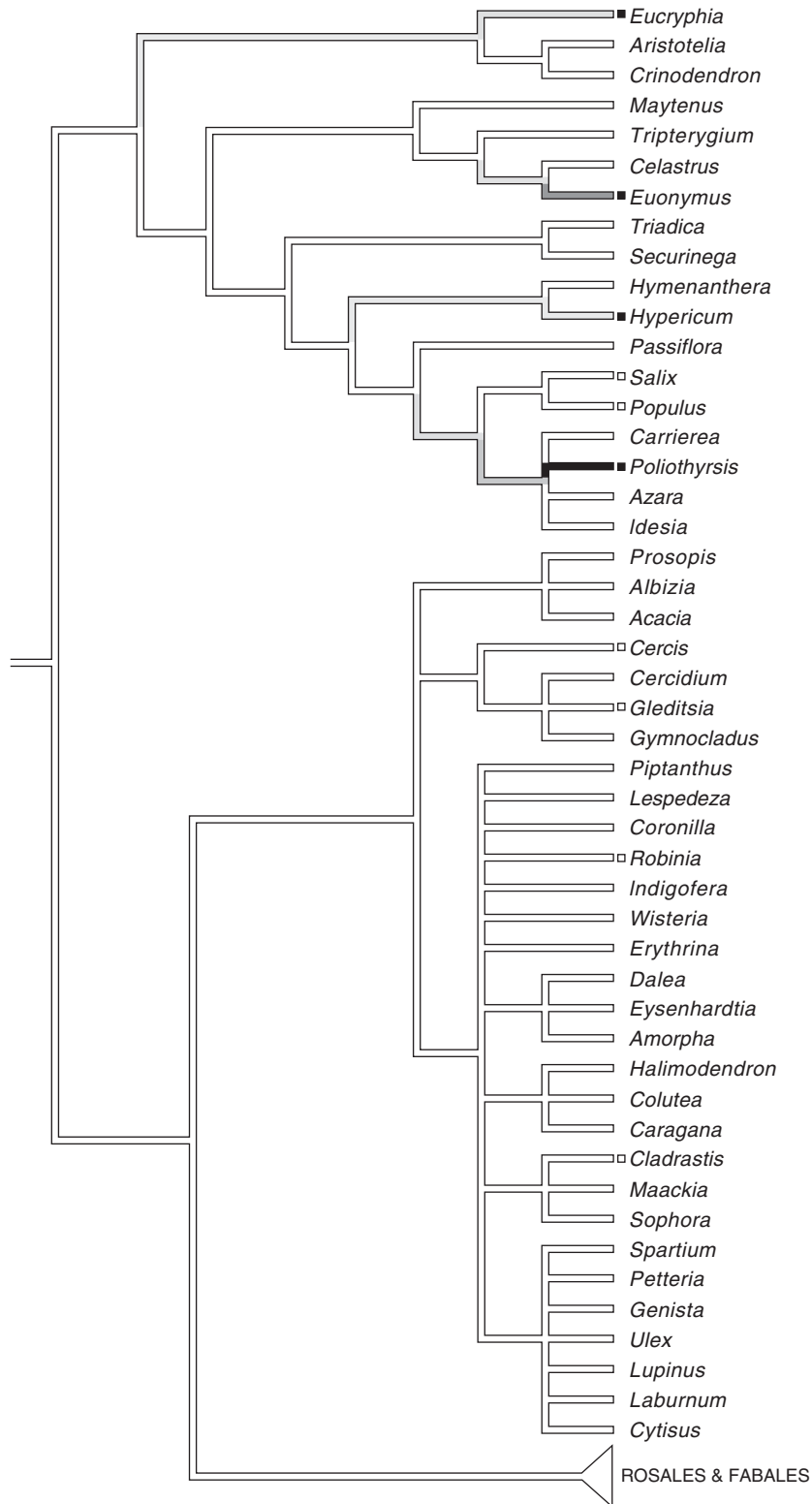


FIG. 6. Eurosid I. Other details as in Fig. 2.

of autumn colours is actually correlated with the presence of aphids in a set of 262 tree species.

If autumn colours are instead an adaptation for photoprotection (Feild *et al.*, 2001; Hoch *et al.*, 2001), then it is possible

that the scattered distribution of autumn colours reflects a different mechanism of photoprotection or a different need of nutrient resorption: species with autumn colours could be the ones that have a greater need to reabsorb nitrogen before

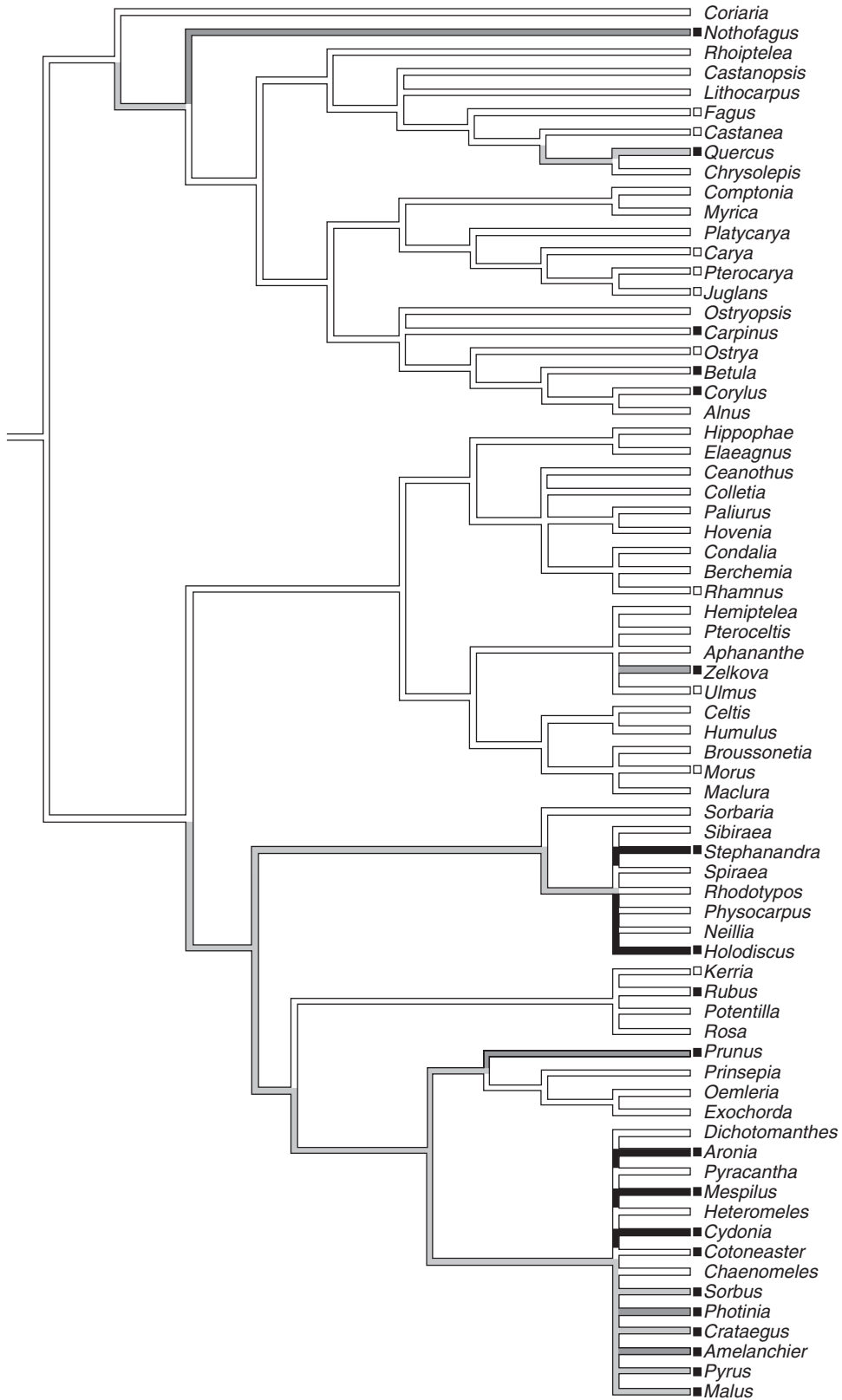


FIG. 7. Rosales and Fabales. Other details as in Fig. 2.

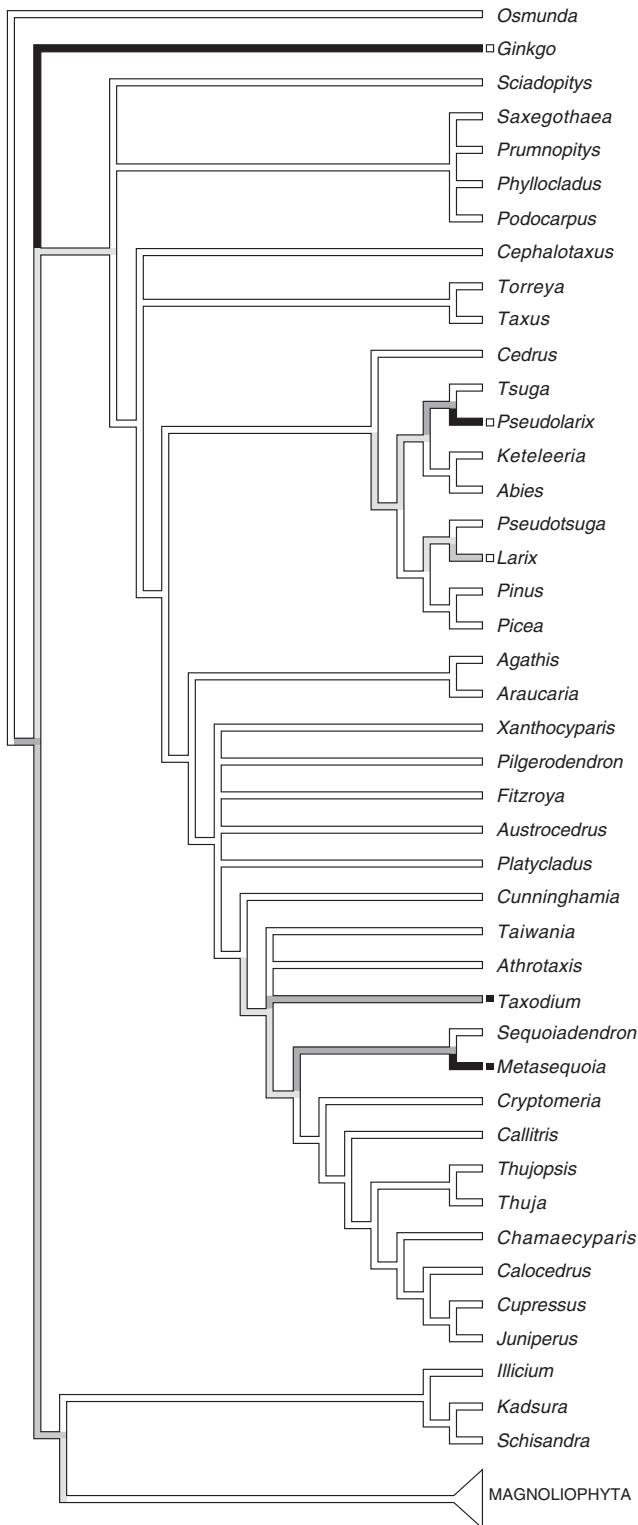


FIG. 8. Conifers. Other details as in Fig. 2, but branches are coloured in grey-scale proportional to the frequency of both red and yellow species.

leaf fall, and therefore for the photoprotection that anthocyanins may provide. One intriguing possibility is that tree species living in symbiosis with nitrogen-fixing bacteria, for example alders (*Alnus*), do not have autumn colours because

they do not need efficient resorption of nitrogen. A comparative analysis of the photoprotection hypothesis does not exist, but it might be attempted now using the data provided here, if nitrogen content can be measured for a large number of species.

Recent research has focused on photoprotection and coevolution, but there are other possible hypotheses (Archetti *et al.*, 2009) relating to, for example, drought resistance (pigments decrease osmotic potential allowing leaves to tolerate water stress), leaf warming (pigments convert light into heat and warm leaves), fruit flag (colour attracts animals that help disperse seeds), camouflage (colour makes leaves less detectable to herbivores), anticamouflage (colour enhances conspicuousness of parasites dwelling on leaves to predators or parasitoids), unpalatability (pigments act as direct anti-feedants against herbivores), reduced nutrient loss (yellow leaves have less to lose against herbivory) and tritrophic mutualism (colour attracts aphids that attract ants that defend the trees from other insects). Assumptions and predictions of these hypotheses are described elsewhere (Archetti, 2009). No comparative analysis (and in most cases no empirical data) exist for these hypotheses.

#### Methodological improvements

A more objective method to measure colour could be used in future studies. Colours (what we call ‘yellow’, ‘orange’, ‘brown’, etc.), are always a categorization that depends on the subjective perception of the observer. Colour perception varies among animals (Briscoe and Chittka, 2001) and even between different human cultures (Saunders and van Brackel, 1997). Therefore, human vision does not provide an objective measure of colour. Likewise, the colour space measured by digital images (RGB, CMYB, or similar) is only a numerical value that corresponds to a scale of colours based on human perception. An objective classification of colour that is independent of the perceiver should be obtained using a spectrophotometer, which allows the display of the distribution of wavelength reflected by an object. Spectral measurements could be translated into photoreceptor responses for a specific observer (e.g. into CIELAB values for human vision) and this would give a measure that could be used to place the object into a colour category (e.g. ‘yellow’ or ‘green’). These categories, however, would still be based on the previous subjective definition of what should be called ‘red’, ‘yellow’, and so on. Human vision, on the other hand, has an advantage in that it allows a large range of spatial integration, which is impossible to achieve using a spectrophotometer, and is particularly important when measuring autumn leaf colours, which vary from tree to tree within the same species, and indeed even from leaf to leaf or within a leaf.

The main shortcoming when using the human eye, instead of a spectrophotometer, is that the resulting categorization would not be relevant for animals with different photoreceptors. An insect with standard blue/UV vision, for example, would probably classify some hues of our (human) red as a different hue of (human) green. Moreover, insects are sensitive to UV light, which humans cannot perceive. In leaves, however, differently from flowers, the reflectance in the UV range is usually a straight horizontal line at only

about 3–10 % reflectance over the entire spectrum between 300 and 400 nm (Döring *et al.*, 2009). In other words UV reflectance in leaves is not very important even for insect vision. It is important to remember, however, that the classification of colours reported here is only relevant for a human observer. A classification using a combination of direct observations by eye and spectral data would be most welcome.

#### Further data and analyses

The list provided here could be expanded and extended to herbs, which also have autumn colours, although probably at lower frequencies than trees (Lee *et al.*, 2003). It is also necessary, in order to test the different hypotheses for the evolution of autumn colours, to have the following data for each tree species: nitrogen content in mature and young leaves (for the photoprotection hypothesis); susceptibility to drought (for the drought resistance hypothesis) and to cold temperatures (for the leaf warming hypothesis); presence of insect pests (not only aphids) migrating to the trees in autumn (for the coevolution, camouflage and anticamouflage hypothesis); concomitant presence of parasitoids (for the anticamouflage hypothesis); presence of direct herbivory in autumn (for the unpalatability and reduced nutrient loss hypothesis); presence of birds and other dispersal agents and presence of fruits ripening in autumn (for the fruit flag hypothesis); and presence of aphids which attract ants (for the tri-trophic mutualism hypothesis).

These data would allow the available hypotheses to be tested. Interspecific comparative analysis is a powerful method for testing adaptive hypotheses in evolutionary biology, and I hope the data presented here will stimulate further research on the evolution of autumn colours.

#### SUPPLEMENTARY DATA

A list of autumn colours for all species considered in this work is available as Supplementary Data at [www.aob.oxfordjournals.org/](http://www.aob.oxfordjournals.org/).

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