



How just a few makes a lot: Speciation via reticulation and apomixis on example of European brambles (*Rubus* subgen. *Rubus*, Rosaceae) [☆]



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ABSTRACT

New species are generated by many means, among which hybridization plays an important role. Interspecific hybrids can form isolated evolutionary units, especially when mechanisms increasing viability and fertility, like polyploidy and apomixis, are involved. A good model system to study reticulate evolution in plants is *Rubus* subgen. *Rubus* (brambles, blackberries), which only in Europe includes 748 accepted species, out of which only four are sexual diploids and all others are polyploid apomicts. We employed two molecular markers (ITS and cpDNA) to shed light on the evolutionary history of European bramble flora and main processes generating such high species diversity. We distinguished just six ancestral diploids (including two extinct ones) for both markers, which gave rise to all European polyploid accessions, and revealed an extreme reticulation in bramble evolution. We furthermore detected hybridogenous origins and identified putative parents for several taxa (e.g. ser. *Nessenses*), while in other groups (e.g. ser. *Discolores*) we could also infer the direction of hybridization. By comparing different cp haplotypes having clear geographic patterns, we hypothesize that the origin of European brambles can be attributed to both Holocene species range expansion and Pleistocene climate fluctuations.

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1. Introduction

Species-rich genera – i.e. large ones containing more than 500 species (Frodin, 2004) – represent up to one quarter of all flowering plant species (Monro, 2006). Besides taxonomic discussions, many factors are thought to underly such systematic patterns, among them life form, mode of dispersal, key innovations, rate of neutral evolution, co-evolution with pollinators and other various biotic and abiotic interactions leading to rapid radiation, divergence and multiple speciation events (Eriksson and Bremer, 1991; Hodges and Arnold, 1995; Rieseberg and Willis, 2007). Hybridization has furthermore played a major role in plant speciation, often in combination with polyploidy, as it ensures rapid reproductive isolation between the hybrid and parental species, usually within one or two generations (Rieseberg and Willis, 2007). On the genome level, it further enhances evolution through gene redundancy and potential subfunctionalization of duplicated genes (Comai, 2005). Moreover, polyploidization, either via somatic doubling, fusion of unreduced gametes or through the so called triploid bridge, can often lead to reduction of maladaptive

changes in gene expression and restoration of hybrid fertility through allopolyploidy-induced sequence elimination or changes in gene expression ameliorated by genome duplication (Rieseberg and Willis, 2007). Nonetheless, meiotic aberrations and associated decreases in fertility, not to mention complete sterility, represent significant obstacles to the establishment of a hybrid lineage (Comai et al., 2003; Comai, 2005). One potential evolutionary solution to this problem is asexual reproduction, either by vegetative means or through seeds (apomixis or agamospermy; Asker and Jerling, 1992).

Apomixis (and parthenogenesis in animals) is typically associated with both polyploidy and hybridity, since many apomictic taxa are of allopolyploid origin (Bicknell and Koltunow, 2004), although it is unclear whether these traits represent cause or effect of asexual reproduction. For example, the widespread occurrence of diploid apomixis in *Boechera* Á. Löve & D. Löve, by definition implicates hybridization rather than polyploidy as the inducer of apomixis from sexual ancestors (Beck et al., 2012), although analyses of genetic variation also demonstrate that diploid apomicts are not always interspecific hybrids (Lovell et al., 2013). Apomixis has also been reported in several autopolyploid taxa, e.g. *Townsendia hookeri* Beaman (Thompson and Whitton, 2006), *Paspalum* L. (Hojsgaard et al., 2008) or *Ranunculus kuepferi* Greut. et Burd. (Cosendai et al., 2011). Hence, depending on the species context,

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hybridization and polyploidy may only indirectly be correlated with apomixis, for example by masking deleterious mutations accumulated during the asexual life cycle.

The adaptive and evolutionary potential of asexuality has historically been underestimated, resulting from the assumption that obligate apomicts are characterized by low genetic variability (Hörandl and Paun, 2007). In contrast, accumulating evidence based upon genetic markers and population genetic methods support the opposite view. As many apomicts are facultative, whereby low levels of sexuality are maintained, backcrossing with sexual relatives is hypothesized to lead to multiple evolutionary origins of apomictic lineages, with the concomitant generation of considerable clonal diversity (van der Hulst et al., 2000; Paun et al., 2006). On the population level, apomictic lineages often show higher levels of genetic variability (e.g. observed heterozygosity) compared to their sexual relatives (Hörandl and Paun, 2007), a reflection of their allopolyploid origin in addition to mutation accumulation (i.e. Muller's ratchet; Muller, 1964), the latter of which generates new alleles which are subsequently redistributed into new genotypes via occasional sexual outcrossing (Asker and Jerling, 1992; Majeský et al., 2012, 2015). Beside fixed heterozygosity, potential hybrid vigor and buffering of inbreeding depression, apomicts can take advantages from uniparental reproduction, lowered cost of sex, maintaining adapted genotypes and at the same time also from reproduction by seeds including dormancy, diaspore protection and better dispersal ability compared to vegetative reproduction (Hörandl, 2006). All these factors can lead to great ecological and evolutionary success of many apomictic plant genera.

The genus *Rubus* L. is a good example of such a successful taxon, being characterized by twelve subgenera and a worldwide distribution (excluding Antarctica). It is widespread across Europe (Kurtto et al., 2010), with some European species having been introduced for fruit production into different parts of the world where they have repeatedly become aggressive invaders (Caplan and Yeakley, 2010; Clark et al., 2013). The taxonomic classification of the enormous number of described species has been a challenging task for generations of researchers. A recent taxonomic approach – referred to as the *Weberian concept* (Weber, 1996) – consider a species only if it is morphologically stable over wider distribution area, and ignores local morphotypes/biotypes of putatively hybrid origin. Although this approach reduced the number of accepted species considerably, 763 *Rubus* species are still recognized in Europe, of which 748 belong to the subgenus *Rubus* (brambles, blackberries; Kurtto et al., 2010). Morphologically similar species are clustered into *series*, which are rather artificial units with overlapping morphology. Further, out of the high number of known species in Europe, only four sexual diploids (i.e. *R. ulmifolius*, *R. canescens*, *R. incanescens* and *R. sanctus*) are known, and additionally four confirmed diploid sexuals occur in neighboring regions of the Transcaucasia (*R. moschus*) and Macaronesia (*R. bollei*, *R. palmensis* and *R. serrae*; Gustafsson, 1942; Matzke-Hajek, 2001; Kurtto et al., 2010). It is likely that this extensive taxonomic complexity is the reason for the absence of any reliable subgenus-wide phylogenetic analysis to date.

The three above mentioned factors – apomixis, polyploidy and hybridization – are the main contributors to such complexity, as the majority of European brambles are tetraploid (with some triploid, pentaploid and hexaploid) pseudogamous apomictic lineages (Krahulcová et al., 2013). Reproduction is highly variable, ranging from obligate sexuality to obligate apomixis on the inter- and intraspecific levels, to the floral level within a single individual or even ovules within a single flower (Pratt and Einset, 1955; Gerlach, 1965; Šarhanová et al., 2012). Apomixis itself can furthermore combine both apospory and diplospory (Christen, 1950; Pratt and Einset, 1955), not to mention that the reproductive mode can

be influenced by external environmental factors (Šarhanová et al., 2012). Especially in tetraploid taxa, the degree of residual sexuality can be considerable, as seen on both seed and seedling levels (Jennings et al., 1967; Nybom, 1995; Kollmann et al., 2000). On the other hand, triploid and pentaploid accessions show almost obligate apomixis (Šarhanová et al., 2012). Additionally, fertilization of unreduced embryo sacs, leading to increased ploidy levels, or spontaneous development of reduced embryo sacs giving rise to polyploid offspring, are sometimes observed in flow-cytometric seed screen analyses of various taxa (Šarhanová et al., 2012) as well as in offspring from artificial crossings (Crane and Thomas, 1949). The fusion of two reduced egg nuclei (i.e. automixis) has also been found (Gerlach, 1965; Antonius and Nybom, 1995).

Batologists (specialists on brambles) have long been aware of hybridization as the main driving force of *Rubus* evolution, as reflected in the overlapping morphology of the various *Rubus* series. Many experimental crosses have shown frequent hybridization even between distant taxa, as the fitness of F1 and subsequent hybrids are very high, sometimes higher than that of their respective parents (Lidforss, 1914; Jennings et al., 1967; Nybom, 1988). These studies have also shown improved meiosis in artificial hybrids (see also Bammi and Olmo, 1966) resulting in higher pollen viability and seed set, as well as in higher degree of sexuality. Early experiments with artificial hybrids additionally revealed enormous morphological variability among hybrid progeny, much of which often resembles distantly related natural taxa (Lidforss, 1914; Rozanova, 1934, 1938). Importantly, these works point out that a given cytologically and morphologically defined polyploid accession can be formed not only multiple times independently, but also in several ways from the same basal ancestors (Mavrodiev and Soltis, 2001). These experimental data have been confirmed for natural populations using molecular markers in several lower-level taxa (Kraft et al., 1995; Alice et al., 2001), although only morphological and cytological evidence has been employed to study wide-scale evolutionary patterns of European brambles.

While much is understood regarding microevolutionary processes and morphological differentiation in *Rubus*, the mechanisms of diversification, especially with regards to which species were (or still are) involved in polyploid evolution in European *Rubus*, remain unclear. In this study, we analyze chloroplast and nuclear DNA markers (Internal transcribed spacer; ITS) in a broad sample covering all major series within the *Rubus* subgen. *Rubus* to understand the evolutionary patterns and processes influencing their evolution, and furthermore we attempt to identify parental species associated with hybridization. While commonly used in phylogenetic studies, ITS is part of highly repetitive tandem rDNA array whose evolution is complicated by processes such as sequence homogenization, intergenic recombination and pseudogenization (Álvarez and Wendel, 2003). These may lead to distortion or even loss of phylogenetic signal in hybrid complexes. On the contrary, it was documented that concerted evolution of ITS is suppressed in polyploid apomicts (genus *Taraxacum*, Asteraceae) preserving high intraindividual variability (Záveská Drábková et al., 2009). Thus we aimed to quantify the intragenomic processes potentially affecting the usefulness of ITS for reconstruction of evolutionary pathways in apomictic genera.

2. Materials and methods

2.1. Plant material

A total of 287 individuals from 145 species were sampled throughout Europe and adjacent regions in order to cover the complete taxonomic complexity of the subgenus *Rubus*, including all

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