Research review

The complex causality of geographical parthenogenesis

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Summary

Asexual organisms usually have larger and more northern distributions than their sexual relatives. This phenomenon, called geographical parthenogenesis, has been controversially attributed to predispositions in certain taxa; advantages of polyploidy and/or hybrid origin; better colonizing abilities because of uniparental reproduction; introgression of apomixis into sexuals; niche differentiation of clones; or biotic interactions. This review on apomictic plants demonstrates that each of these factors alone has not been able to explain the observed distributions. Establishment of the complex regulatory system of apomixis requires taxonomic and geographical predispositions; hybridization and/or polyploidization do create diversity, but they do not necessarily result in large distributions; colonizing abilities depend on clonal diversity and are outweighed by sexuals by self-compatibility and higher potentials for speciation; niche differentiation, ploidy levels and selfing keep sympatric sexuals and apomicts separated; and the impact of biotic interactions on distributions is uncertain. In conclusion, the distributional success of apomicts has a complex causality and depends on certain circumstances and combinations of factors. The rare establishment of apomixis may help to explain the predominance of sexuality on the large scale.

Introduction

Apomixis (here defined as agamospermy, i.e. asexual reproduction via seeds) frequently results in considerable abundance and distributional success of some groups, such as dandelions (*Taraxacum*), blackberries (*Rubus*) and grasses (e.g. *Poa*, *Elymus*), challenging the general question of the evolutionary potentials of asexuality. The phenomenon that related asexual and sexual taxa have different distributional patterns has long been recognized, but it is still not well understood. Since Vandel (1928) coined the term 'geographical parthenogenesis', several authors have described the phenomenon both in animals and plants (Bell, 1982; Bierzychudek, 1985; Asker & Jerling, 1992; Van Dijk, 2003; Haag & Ebert, 2004; Kearney, 2005). For higher plants, Bierzychudek (1985) provided the most comprehensive evaluation of the previous literature, and concluded that apomictic plant groups (1) have larger distributional ranges, often considerably exceeding that of their sexual relatives; (2) tend to range to higher latitudes and altitudes than their sexual relatives; and (3) tend to colonize previously glaciated areas. Later studies add the aspect that sexual relatives often have distributions centred within much larger ranges of apomictic

complexes (*Antennaria*, Bayer, 1990; *Stevia*, Soejima *et al.*, 2001; *Paspalum*, Urbani, 2002; *Taraxacum* and *Chondrilla*, Van Dijk, 2003; *Ranunculus*, Hörandl & Paun, In press; earlier studies reviewed by Asker & Jerling, 1992). Asker & Jerling (1992) noted that abundance of apomicts decreases from the south to the north, but increases in northern regions only relative to the rest of the flora. They also discussed the difficulty of direct floristic comparisons because neither agamic complexes nor agamospecies are taxonomically equivalent to sexual species. Richards (1997) pointed out that geographical parthenogenesis applies only to taxa with gametophytic apomixis. Sporophytic apomixis, which is frequently observed in multiseeded tropical plants, and has completely different developmental and control mechanisms, is connected with other ecological and geographical features. This mode of reproduction, and also vegetative propagation, will not be discussed further here.

A broad evaluation of hypotheses to explain possible causes of geographical parthenogenesis led Bierzychudek (1985) to the conclusion that distributional success might be mainly caused by advantages of polyploidy, which is found in almost all apomictic plants. The most recent review by Kearney (2005), based mainly on data from asexual animals, reports basically the same features of distributions, but stresses the importance of advantages connected with hybrid origin as the main causal factor for distributional patterns. Several other nonexclusive hypotheses have been proposed for the causality, relying either on intrinsic features of asexual reproduction such as uniparental reproduction (Stebbins, 1950; Baker, 1967; Mogie *et al.*, In press), or interactions between sexuals and apomicts (Mogie, 1992; Mogie *et al.*, In press); or on external factors such as the production of generalists (general-purpose genotypes, Baker, 1965; Lynch, 1984) vs specialized genotypes (Vrijenhoek, 1984), or biotic interactions with other organisms (Maynard Smith, 1978; Bell, 1982; Glesener & Tilman, 1987).

In higher plants, considerable information about the functionality and genetic control of apomixis has been accumulated in recent years, factors that have not often been considered geographical questions. Because of high frequencies of hybridization and polyploidy, plants are ideal model systems for discussion of these two factors. Because of some features of plant reproduction, asexual reproduction appears to be less advantageous in plants than in animals. (1) Because of the predominance of hermaphroditism, most plants do not have the frequently cited 'cost of sex' from producing male individuals (Maynard Smith, 1978); the costs of the male function are only of male organs. A resource allocation from male to female reproduction has been observed in rare cases of male sterility (Meirmans *et al.*, 2006), but the majority of apomicts maintain the male function for fertilization of primary endosperm nuclei, which is required for formation of viable seed (pseudogamy). (2) Vegetative reproduction and self-fertilization outweigh expected advantages of uniparental reproduction for apomicts. In hermaphroditic plants, both selfing and apomixis avoid the 'cost of outcrossing', that is, selfers and apomicts can serve as

pollen parents of progeny of outcrossers, but not *vice versa* (Holsinger, 2000).

Previous authors have emphasized that geographical parthenogenesis is probably caused by a combination of factors (Haag & Ebert, 2004; Pound *et al.*, 2004; Mogie *et al.*, In press). Consequently, the main focus of this review is to evaluate the causality for the phenomenon in angiosperms by discussing all possible factors shaping distributions: to what extent a factor can act alone and is compensated by modifications of the sexual pathway; how combinations of factors are effective; and the implications of conclusions for the evolutionary potentials of asexuality.

Geographical parthenogenesis and the origin of asexual reproduction in plants

For an understanding of the biogeographical histories of apomictic complexes, the locations, circumstances and mechanisms of *de novo* origins of apomixis are of interest. Geographically, sexual relatives of apomictic complexes have predominantly temperate to boreal distributions. Apomixis is thought most likely to arise in areas and time periods influenced by glaciations of the Pleistocene, where range fluctuations of plants because of climatic oscillations offered the most frequent opportunities for interspecific hybridization (Lynch, 1984; Carman, 1997). Recent molecular studies confirm a relationship of the origin of apomictic lineages with the Pleistocene or postglacial time periods (Bayer, 1990, 1991; Dobeš *et al.*, 2004a; Paun *et al.*, 2006b).

Increasing understanding of the mechanisms of apomixis has given insights into not only functionality, but also the frequencies and circumstances of *de novo* origins of apomixis. It is well established that apomixis is heritable and under control of one or more Mendelian factors, and that it is a modification of the sexual pathway, rather than an independent trait. Three independent processes, not controlled by the same loci (Mogie, 1992; Grimanelli *et al.*, 2001; Spielmann *et al.*, 2003; Bicknell & Koltunow, 2004), must act together for the production of functional apomictic seeds: development of (1) an unreduced embryo sac bypassing meiosis (apomeiosis, via diplospory or apospory); (2) the egg cell without fertilization (parthenogenesis) to avoid increase of ploidy levels; and (3) a functional endosperm (Fig. 1).

Several different hypotheses have been proposed for the origin of apomixis (Koltunow & Grossniklaus, 2003): (1) that apomixis is caused by mutations in one or a few linked genes, or in a master gene that initiates the different elements in a cascade-like fashion; (2) that apomixis-specific factors in supernumerary chromatin would control apomixis; (3) that stable and heritable epigenes could arise after hybridization and/or polyploidy through changes in DNA methylation or chromatin structure; and (4) the hybridization-derived floral asynchrony (HFA) theory, that the combination of genomes of two parental ecotypes differing in timing of developmental pathways would
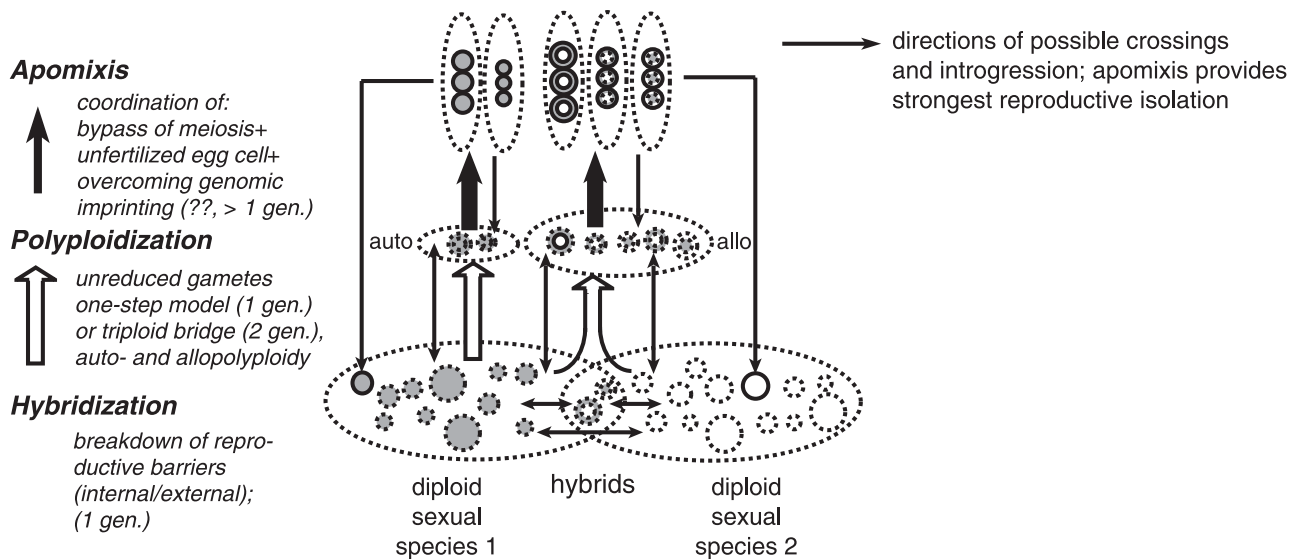
Fig. 1 Scheme of the evolutionary processes and required steps involved in hybridization, polyploidization and apomixis in higher plants; minimum number of generations (gen.) required in parentheses (after Asker & Jerling, 1992; Ramsey & Schemske, 1998). Different degrees of reproductive isolation are shown by arrows indicating possible pathways of backcrossing.

lead in the duplicated genome to an asynchronous expression of wild-type genes that regulate the steps from meiosis to post-fertilization. This would result in precocious embryo sac initiation and parthenogenetic embryogenesis (Carman, 1997, 2001). The idea is supported by observations that the timing of developmental steps influences frequencies of apomictic phenotypes (Grimanelli *et al.*, 2003).

Models 1 and 2 would require at least one mutation for apomeiosis and a coordination with parthenogenesis (Mogie, 1992; Grimanelli *et al.*, 2001), or two independent mutations for both traits, both being individually deleterious (review in Van Dijk & Vijverberg, 2005), plus overcoming imprinting barriers for endosperm development (Spielmann *et al.*, 2003). In fact, a complex of closely linked genes may control apomixis (Van Dijk & Vijverberg, 2005), which is supported by recent findings that in *Poa pratensis* five independently segregating major genes control apomixis (Matzk *et al.*, 2005). It is unlikely that such complex changes for the origin of apomixis have happened frequently. In fact, apomixis occurs multiple times within angiosperms (Van Dijk & Vijverberg, 2005), within genera and also within complexes (Sharbel & Mitchell-Olds, 2001; Fehrer *et al.*, 2005), usually in evolutionarily advanced groups, but restricted to certain orders and families (Van Dijk & Vijverberg, 2005). Epigenetic changes (models 3 and 4) are heritable, and might also arise easily after hybridization or polyploidization (Koltunow & Grossniklaus, 2003), often altering temporal, spatial and abundance patterns of gene expression (Rapp & Wendel, 2005). Nevertheless, the processes resulting in simultaneous establishment and appropriate timing of the three components mentioned above, and the connection to polyploidy and hybridization, are still not well understood. Apomixis can arise in autopolyploids within the

same species (Yahara, 1990; Bayer, 1991), and can be induced by artificial autopolyploidization without any combination of different genomes (Quarin *et al.*, 2001). Apomixis also occurs rarely in diploids (e.g. in *Boechera holboellii*, Sharbel & Mitchell-Olds, 2001), although this may, in fact, be a paleopolyploid (Bicknell & Koltunow, 2004). In contrast, apomixis does not appear in F_1 hybrids of sexual relatives of apomictic complexes (Asker & Jerling, 1992). Apomixis is perhaps most frequently (but not necessarily) connected with hybridization and polyploidy, because the combination of both traits increases the likelihood of the required complex changes of genetic control (U. Grossniklaus, personal communication).

Despite considerable efforts and intensive research over decades, induction or transfer of apomixis into crops has so far had limited success (reviews in Savidan *et al.*, 2001), confirming a high complexity of regulatory mechanisms. This is probably a main reason for its rare establishment, arising in less than 1% of angiosperm species (Mogie, 1992), despite the fact that that polyploidy and hybridization are frequent phenomena in higher plants (Table 1). Approximately 75% of apomictic taxa belong to only three families (Asteraceae, Poaceae and Rosaceae; Richards, 1997), which has been attributed to predispositions of some families either to overcome imprinting barriers in the endosperm, or to bypass fertilization of the endosperm via autonomous apomixis (Spielmann *et al.*, 2003; Bicknell & Koltunow, 2004). Another hypothesis suggests common ancestry and introgression of apomixis genes at (sub)tribal level within these families (Van Dijk & Vijverberg, 2005). A third idea relates apomixis to predominance of single-seeded fruits in these families (e.g. achenes, caryopses), which could infer selective fitness advantages of asexually produced, separated seeds and seedlings (Richards, 1997).

Table 1 Summary of advantages and disadvantages of reproductive systems and evolutionary traits in angiosperms: estimates of frequencies among angiosperm species (in parentheses) demonstrate the rarity of establishment of apomixis

Mode	Advantages	Disadvantages
Sexual selfer	Uniparental reproduction, reproductive assurance; frequent (as dominant approx. 20%; as casual approx. 40%)*, high flexibility	Increased homozygosity, inbreeding depression
Sexual out-crosser	Maintenance of genetic diversity	Mating partner and pollinator needed
Hybridization	Novel genomic composition, possible transgressive segregation	Minority type, reduced fertility; without polyploidy, lack of reproductive isolation against the parents; infrequent (7–11%)†, easily formed but difficult to establish
Polyploid sexual	Novel genomic composition, fixed heterozygosity, often self-compatible, reproductive barrier against parents, high frequency (40–70%)‡, easily formed and established	Functional disturbances of meiosis and gene expression possible, aneuploidy
Apomict	Reproductive isolation, uniparental reproduction, reproductive assurance, heterozygosity	Reduction of genotypic diversity, low adaptive potential, difficult to form and establish, less than 1%§

*After Richards (1997).
†Based on estimates for instances of hybrids in general, reviewed by Ramsey & Schemske (1998).
‡After Ramsey & Schemske (1998).
§After Mogie (1992).

Concluding, apomixis arises not randomly, but requires the simultaneous establishment of complex genetic and/or epigenetic regulatory mechanisms, which require taxonomic, geographical and ecological predispositions. Considering the rather young geological age of apomicts, their higher abundance at higher latitudes/altitudes may simply reflect preferences for macroclimatic conditions similar to those of their ancestors and their main areas of historical origin.

Polyploidy and/or hybridization as causal factors of geographical parthenogenesis

Bierzychudek (1985) hypothesized that the distributional success of apomicts is simply caused by advantages of polyploidy. Multiple copies of the genome provide pathways for development of new gene functions, and combination of genetic information from different ancestors, thus providing more physiological and ecological flexibility compared with their diploid parents. Recent surveys have confirmed extensive effects on restructuring of genomes following polyploidization because of massive gene silencing, diversification in gene function, and different expression of parental genes (Adams & Wendel, 2005). Nevertheless, polyploidy also has negative effects, such as disrupting impact on nuclear and cell enlargement; the propensity of polyploids to produce aneuploid cells; and epigenetic instability in transgressive (nonadditive) gene regulation (Comai, 2005). Polyploids can be formed rapidly in higher plants by unreduced gametes, either via one-step formation or via the triploid bridge, with or without interspecific hybridization; estimates of frequencies among angiosperm species range between 40 and 70% (Ramsey & Schemske, 1998).

Nevertheless, polyploid taxa do not necessarily show broader distributions than diploids. After examination of 75 polyploid complexes in European genera, Stebbins & Dawe (1987) observed that, in 69 genera, the ratio of widely distributed to narrowly distributed species is not significantly higher in polyploid species than among diploid species of the same genus. They concluded that broad distributions are not a universal tendency of polyploids, but must also be attributed to other features. Autopolyploid sexual cytodemes may have much smaller distributional areas than the diploids of the same species, as shown for example in *Ranunculus cassubicifolius* (Hörandl & Greilhuber, 2002). Even in northern areas, where polyploidy is increasing in frequency and levels towards the north (Brochmann *et al.*, 2004), polyploid species do not necessarily have wide distributions. Diploid sexual endemic vascular plants of the North Atlantic area do not show significant differences from polyploid sexual species in the size of distributions, estimated as the number of floristic regions occupied (Fig. 2; Brochmann *et al.*, 2003).

It is difficult to test whether a diploid apomict has a narrower distribution than a polyploid, as would be expected, because such cases are extremely rare. In *Boechera holboellii* (= *Arabis holboellii*), apomixis occurs both in diploid and polyploid cytodemes, sexuality only in diploids; surprisingly enough, diploids show broader distributions and are substantially more frequent within previously glaciated areas than polyploids (Dobeš *et al.*, 2004a, 2004b). These findings suggest that polyploidy alone, although an important mechanism for speciation and diversity in the north, cannot explain the striking range expansions of apomictic complexes compared with their sexual relatives.

Excluding interspecific hybridization, apomictic autopolyploid cytodemes of two *Antennaria* species (Bayer, 1991) and *Boehmeria spicata* (Yahara, 1990) have larger and, at least in *Antennaria*, more northern distributions than diploid sexual
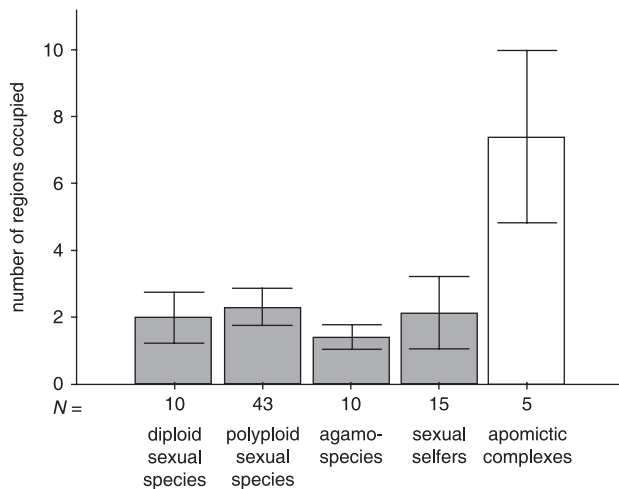
Fig. 2 Number of floristic regions occupied by endemic species (closed bars) and whole nonendemic apomictic complexes (open bar) of the North Atlantic region, mean values (bars) and 95% CI (data from Brochmann *et al.*, 2003; total number of regions = 9; all questionable cases excluded). Pairwise differences (diploid vs polyploid sexuals; agamospecies vs selfing taxa; agamospecies vs polyploid sexuals) are not significant (one-way ANOVA, $P > 0.05$).

cytodemes of the same species. That means a combination of polyploidy plus apomixis, without interspecific hybridization, can be effective for geographical parthenogenesis.

Excluding polyploidy, homoploid hybridization results in sexual plants not frequently in distribution areas separated from that of the parents. Floristic surveys such as that of Stace (1976) show that homoploid hybrids occur in the majority of cases just locally among their parents, as a result of multiple local origins rather than dispersal of single hybrids. Introgressive hybridization may form hybrid zones that are often not well defined geographically, frequently at ecotones or boundaries between habitats in the sympatric range of the parental species (Harrison, 1993). Introgression may occasionally result in replacement of one or both parents, but rarely in distributions distinct from the parents. A review of 165 'noteworthy' case studies of widespread diploid, introgressive hybridization (definitely excluding only local hybrid swarms) demonstrates that only a minority of studies (*c.* 40%) suggest evolution of new ecotypes or species (Rieseberg & Wendel, 1993). Diploid hybrid speciation is, in general, regarded as rare (Wolfe *et al.*, 1998a, 1998b and literature therein), and is often attributed to transgressive segregation and ecological speciation (Seehausen, 2004). In well documented cases of homoploid hybrid speciation, such as in North American irises (Arnold & Bennett, 1993); sunflowers (Rieseberg *et al.*, 2003); and *Penstemon* (Wolfe *et al.*, 1998a, 1998b), homoploid hybrid species show a differentiation of habitats or pollinators, but their distribution areas remain much smaller than those of the parental species; a northern tendency is not observed.

Concluding, hybridization alone is not correlated with significant range expansions outside the distribution area of the

parents and towards the north, as is typical for geographical parthenogenesis. Hybridization creates genomic novelty, but requires a stabilizing mechanism providing reproductive isolation, such as polyploidy, chromosomal recombination, or external barriers (Grant, 1981). Hybrids have to overcome disadvantages of reduced fertility and of a minority cytotype among the parents (Levin, 2002). Apomixis provides a threefold solution for these problems: first, it prevents fertilization and introgression by sexuals (but allows introgression of apomicts into sexuals, see below and Fig. 1); second, potential meiotic disturbances following hybridization and/or polyploidy are not effective; and third, it avoids the necessity to build up populations to maintain certain genotypes and allows dispersal of single clones (see below). In this combination, apomixis can be more successful than sexual allopolyploidy, which has similar potential: large pools of genotypes and phenotypes with novel evolutionary trajectories (Arnold, 1997), and fixed heterozygosity (Brochmann *et al.*, 2004). But the strong correlation with large range expansions compared with diploid sexual relatives, as observed in apomictic complexes, is not evident in sexual allopolyploid species. Therefore geographical parthenogenesis is better explained by a combination of novel genotype/phenotype, reproductive isolation provided by apomixis, plus uniparental reproduction promoting extensive range expansions. The latter is discussed in the following section.

Advantages of uniparental reproduction for colonization

Compared with vegetatively reproducing plants, apomicts benefit from advantages of reproduction via seed such as specialized dispersal mechanisms, protection, seed dormancy, and freedom from disease in vascular strands (Richards, 2003). Apomicts have often been thought to be better colonizers than sexual outcrossers, especially after long-distance dispersal, because of uniparental reproduction, similar to selfing plants (Stebbins, 1950; Baker, 1967, 'Baker's law'), because of the potential to found populations with single individuals (Fig. 3a). Sexual relatives of apomicts are usually self-incompatible (Asker & Jerling, 1992). In contrast, apomicts reproduce either independently from pollination (via autonomous apomixis), or via pseudogamy. In the latter case, self-pollination enables the development of functional seed even without pollinators (observed in *Ranunculus*, Rutishauser, 1954; Hörandl, unpublished data; and in *Rubus*, Nybom, 1986; Kollmann *et al.*, 2000). For both autonomous and pseudogamous apomicts, numerous molecular studies, even using highly sensitive markers, have confirmed the existence of populations consisting of only one lineage, suggesting that single individuals may indeed have founded such populations (Gornall, 1999; Hörandl & Paun, In press). Moreover, independence from cross-pollination provides reproductive assurance in environments where pollinators are less frequent. As apomicts are usually insect-pollinated, uniparental reproduction may contribute to the success of
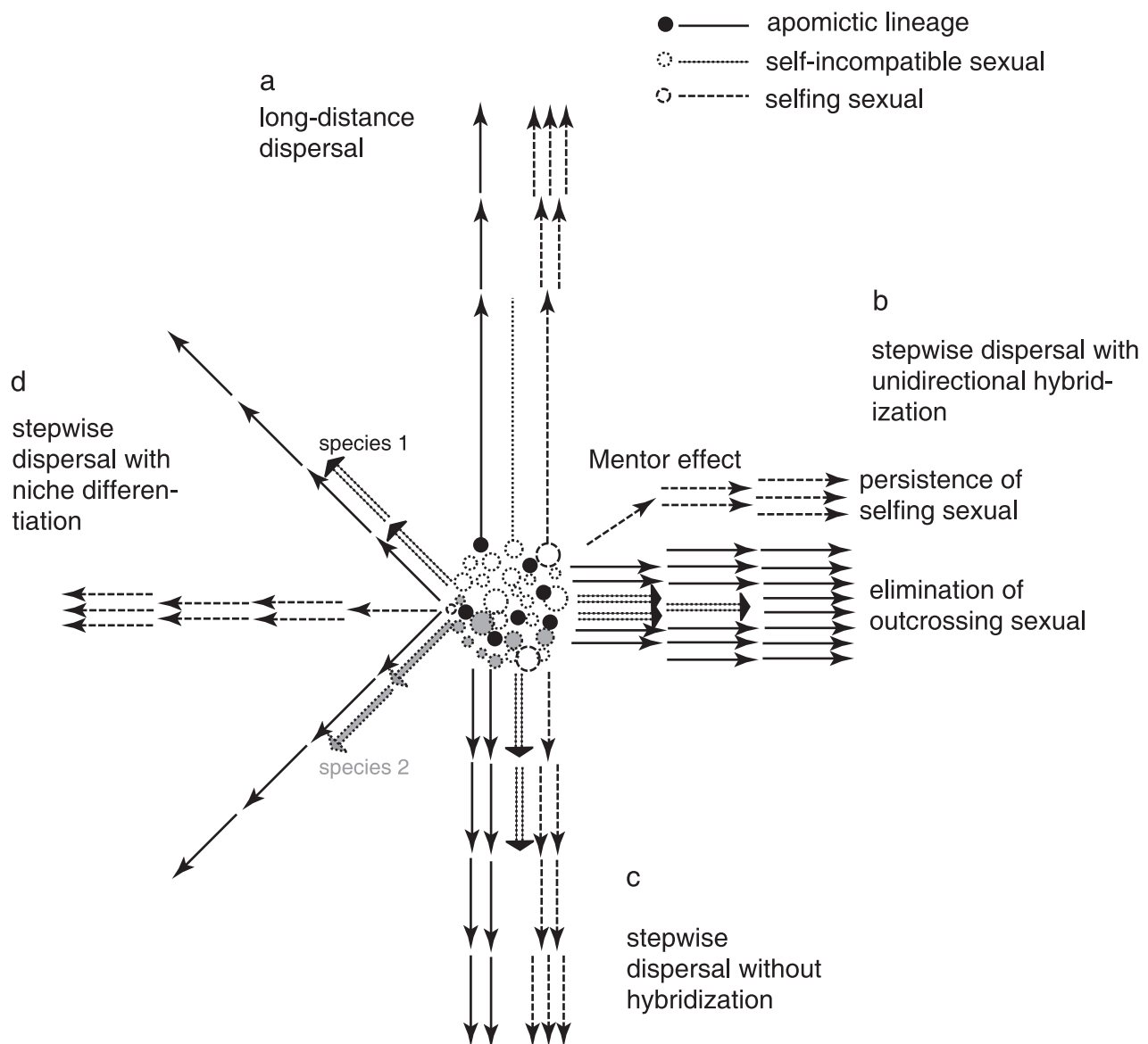
Fig. 3 The impact of reproductive systems on dispersal processes, exemplified in four theoretical scenarios, each starting from a sympatric situation of sexuals and apomicts. Estimated genotypic diversity is symbolized by the number of arrows. (a) Long-distance dispersal of single individuals; apomicts and selfers found new lineages, the latter more quickly re-establishing genotypic diversity. (b) Stepwise comigration with genetic assimilation of sexuals by apomicts via unidirectional gene flow; mixed pollen can turn self-incompatible sexuals to selfing (mentor effect) and avoid extinction. (c) Stepwise comigration without gene flow in the same ecological niche, the apomicts and selfers simply being faster than a self-incompatible sexual because of uniparental reproduction. (d) Niche differentiation: apomictic lineages of hybrid origin are assumed to occupy mainly the niches of the parental species; selfers, novel niches. In all four scenarios the advantage of apomixis is compensated if the sexual species is capable of selfing.

apomicts in regions with colder climates and shorter vegetation periods.

In contrast to selfing plants, apomicts bypass meiosis and avoid increased homozygosity in the offspring. Increased levels of observed heterozygosity have been documented in many apomicts in numerous molecular studies, and are attributed to allopolyploid origin, fixed heterozygosity in duplicated loci, and independent mutations in different alleles (reviewed by Gornall, 1999; Hörandl & Paun, In press).

Hybrid vigour and buffering of inbreeding depression are important effects of heterozygosity; fixed heterozygosity in polyploids may suggest important advantages for colonization (Brochmann *et al.*, 2004). Nevertheless, apomicts of autopolyploid origin do not have significantly higher levels of heterozygosity than their diploid sexual relatives, but do express geographical parthenogenesis (Yahara, 1990; Bayer, 1991; Hörandl & Paun, In press). Theoretically, apomicts are also unaffected by small population sizes and founder effects during initial phases of

colonization, in contrast to outcrossing or selfing sexual species (Barrett & Pannell, 1999). In the long term, apomicts are expected to need a longer time than selfers to recover genetic variation after a bottleneck, because the latter maintain segregation at heterozygous loci during meiosis (Fig. 3a), which will create more variability posed to selection than multiple chromosomes (Burt, 2000). In sexual selfers, selection against homozygous deleterious alleles may lead to purging effects and subsequent increase of fitness after inbreeding (Carr & Dudash, 2003).

Selfing occurs as dominant in *c.* 20%, and as casual in *c.* 40% of angiosperms (Richards, 1997), offering a more frequent and flexible mode of uniparental reproduction. Polyploidization frequently causes a breakdown of self-incompatibility (Marble, 2004; Comai, 2005). Selfing is often associated with an annual life form, which infers an advantage for pioneer plants, but also occurs frequently in perennial colonizers of previously glaciated areas and in island plants (Richards, 1997). Comparisons with self-compatible species considerably restrict generalizations about the superior colonizing abilities of apomicts. In the North Atlantic area, despite the considerable dispersal capacity of endemics, apomictic vs selfing endemics show no significant differences in the number of subregions occupied (Fig. 2, data from Brochmann *et al.*, 2003); but only among selfers some widespread species, occurring in up to seven of the nine subregions, are reported.

Better founder abilities of apomicts are also questioned by habitat preferences and distribution patterns. Despite expected advantages, even to selfing plants, a high frequency of apomicts in open pioneer habitats, such as ruderals, is not observed; instead, in northern Europe, apomictic plants occur most frequently in pastures and on forest floors, in moderately disturbed habitats, where they are significantly more abundant than the rest of the flora (Asker & Jerling, 1992).

The great majority of apomictic clones (92–100%), as assessed by highly sensitive markers, are restricted to single sites (Palacios & Gonzalez-Candelas, 1997; Carino & Daehler, 1999; Van Der Hulst *et al.*, 2000; Houliston & Chapman, 2004; Hörandl & Paun, In press; Paun *et al.*, 2006a). Widespread apomictic genotypes appear just in studies using low numbers of loci, which may underestimate clonal diversity (e.g. isoenzymes), and even then at very low frequencies (Gornall, 1999). In well sampled areas, such lineages generally show continuous distributions without disjunctions (Bayer, 1990; Battjes *et al.*, 1992; Kraft *et al.*, 1996; Hörandl *et al.*, 2001), a feature also generally observed in agamospecies (Fröhner, 1990; Weber, 1995; Tyler, 2000; Brochmann *et al.*, 2003). These distribution patterns and centred small distribution areas of diploid sexual taxa suggest a predominance of recurrent formation of new lineages, and stepwise dispersal processes involving a broad array of genotypes, instead of the success of single clones.

High colonizing abilities after geographical isolation are also questioned by the scarcity of records of apomicts on islands (Bierzychudek, 1985), where long-distance dispersal is required

to overcome geographical barriers. The assumed advantages of uniparental reproduction are confirmed by observations that self-compatibility and self-fertilization are common in island plants, and also occur frequently in island endemics (Barrett, 1996; Anderson *et al.*, 2001). Nevertheless, species diversity of native apomicts on islands compared with the continents is low, even in well documented flora and climatic regions where apomicts are expected to be frequent. In the Flora Nordica region, agamospermous taxa are by far the largest element among Nordic endemics; but among 39 selected endemic agamospecies of the region, only two (5.1%) occur on islands (Jonsell & Karlsson, 2004). In the North Atlantic area, the hugely widespread apomictic complexes *Alchemilla* sect. *Vulgares*, *Hieracium* and *Pilosella* are missing in subregions 1, 2 and 5, respectively, isolated by the Atlantic (Brochmann *et al.*, 2003, Appendix). Only *Taraxacum* and the *Ranunculus auricomus* complex occupy all subregions. The latter group comprises *c.* 600 agamospecies in the Flora Nordica region, and is abundant on the whole continental area (Ericsson, 2001). In contrast, just two agamospecies are certainly island endemics, and abundance of *R. auricomus* s.l. on the Faroer Islands, Svalbard, and most parts of Iceland is drastically reduced to fewer than 10 localities per subregion (Ericsson, 2001). Biogeographical studies on *Hieracium* in northern Europe confirm that all water surfaces provide important dispersal barriers for agamospecies (Tyler, 2000). On New Zealand, apomixis has been assessed so far for just five native species in three genera, whereby this reproductive system has not been widely examined in the native flora (Heenan *et al.*, 2002, 2003). In the well studied flora of the Juan Fernández Islands, agamospermy has been found in only two native dandelions, whereas self-compatibility is reported for 18 species (Bernardello *et al.*, 2001). Among endemics of this island, 81% are self-compatible, but no case of apomixis could be ascertained (Anderson *et al.*, 2001). Nevertheless, rapid range expansions of apomicts on islands are reported after human introductions (Carino & Daehler, 1999; Houliston & Chapman, 2004). Multiple introductions and cases of hybridization of previously isolated species triggered the evolution of new genotypes and rapid speciation on islands (Chapman *et al.*, 2000; Amsellem *et al.*, 2001; Trewick *et al.*, 2004).

The origin of agamospecies is caused by hybridization and/ or polyploidy, which is not a common mode of speciation on islands (Stuessy *et al.*, 2006), and is more likely on the continents because of the higher pool of potential sexual parents and the impact of glaciations. In contrast, island endemism often results from anagenetic speciation (Stuessy *et al.*, 2006), which is not effective in apomicts because of low levels of genetic drift and genotypic variation on which selection can act. Contrary to sexuals, apomictic lineages have a low potential to speciate after strong geographical isolation. Their ability to respond to different environments probably relies on phenotypic plasticity rather than on adaptation.

To summarize: a theoretical advantage of apomixis for colonization can be outweighed by the more flexible system of self-fertilization. The low representation of native apomictic plants in pioneer habitats and in strongly geographically isolated areas contradicts the idea that apomixis suggests a general advantage for founder events. Colonizing success of apomictic complexes appears to depend on the potential to maintain or create a diversity of lineages, which is better achieved on the continent of their origin. Apomixis is probably helpful for range expansions and colonization, but only under certain conditions: (1) self-incompatibility of the sexual competitor; (2) a certain level of initial clonal diversity involved in colonization events; (3) opportunities for recurrent formation and stepwise dispersal; and (4) availability of certain types of habitat.

The male function in asexuals and replacement models

As apomictic plants arise from sexual ancestors, they are expected to occur initially sympatrically with sexual relatives. Most apomictic plants are hermaphrodites, and maintain microsporogenesis via meiosis and production of pollen, which is usually partly, but almost never completely, aborted. In a mixed sexual/apomictic population, a hermaphroditic apomict will also fertilize sexual individuals and transfer apomixis to sexuals via pollen, but will not be fertilized by the sexuals; as mother plants, apomicts have maternal, apomictic offspring. Thus theoretically there is a 1.5-fold advantage to apomixis per generation, and genetic factors controlling apomixis will soon increase in frequency and come to fixation (Mogie, 1992; Fig. 3b). This theoretical assumption will hold if male and female fitness of sexual and apomicts and all other factors are equal. In fact, crossing barriers because of different ploidy levels and/or ecological differences of apomicts and sexuals, facultative sexuality and aborted pollen in apomicts, reduced fitness of F_1 hybrids, and variance in female fitness of apomicts may influence the actual frequencies of reproductive systems. During comigration, extinction of sexuals via introgression may build up a front of apomicts impermeable for sexuals (Mogie, 1992). Immigration of maladapted genotypes into a new environment could result in a loss of fitness in sexuals because of random mating, whereas this is not effective in apomicts (Peck *et al.*, 1998).

Experimental studies in *Hieracium* (Krahulcova *et al.*, 1999) and *Taraxacum* (Morita *et al.*, 1990; Tas & Van Dijk, 1999; Brock, 2004) have shown that self-incompatibility of sexual taxa can break down when accompanied by additional pollen from another sexual or apomictic species (mentor effect, Richards, 1997). Thus sexuals coexisting with apomicts or other closely related species may reproduce via selfing as well, and avoid genetic assimilation by apomicts (Fig. 3b). In mixed populations, selfers also avoid the 'cost of outcrossing' and are expected to reproduce as successfully as apomicts (Holsinger, 2000).

A study on mixed populations of native sexual *Taraxacum ceratophorum* and introduced apomictic *T. officinale* suggests partly genetic assimilation of sexuals because of asymmetrical hybridization, but also partly selfing because of a mentor effect (Brock, 2004).

The HFA theory (Carman, 1997) requires hybridization of ecotypes with different preferences of altitudes/latitudes for the origin of apomixis. Apomixis is probably advantageous in high altitudes/latitudes because of reproductive assurance when pollinators are rare, and a shortening of reproductive pathways (Mogie, 1992). Thus, during colonization of such areas, the apomict competes directly, mainly with the high-altitudinal/latitudinal sexual parent. In the case of missing niche differentiation, the apomict may replace the high-altitudinal/latitudinal sexual because of unidirectional hybridization. Only the more southern/lowland parental sexual would persist, which would fit with observed distribution patterns. This would explain the high relative frequency of apomixis in northern regions without the necessity of colonizing extremely high latitudes/altitudes or open pioneer habitats; in temperate regions with longer vegetation periods, the advantage of apomixis may be less important.

The big problem of replacement models is to explain the frequently observed coexistence of sexuals and apomicts, in other words, why sexuals have not gone extinct completely. Simulation studies on small-scale spatial dimensions in the form of patchy occupancy models of mixed sexual–asexual populations suggest that one of the reproductive modes comes to fixation in the landscape because of formation of clusters, whereby initial conditions are probably important. Nevertheless, examples of coexistence are also found in theoretical modelling (Carillo *et al.*, 2002). Empirical studies in mixed apomictic/sexual populations are rare, but suggest coexistence because of niche differentiation (see below), and reproductive isolation via different ploidy levels (Vavrek *et al.*, 1998; Hörandl *et al.*, 2000; Meirmans *et al.*, 2003; Verduijn *et al.*, 2004; Fig. 3c). To conclude, replacement of sexuals by apomicts via introgression is probably limited by (1) the strength of reproductive barriers; and (2) the capacity of sexuals to shift to selfing.

The general-purpose genotype vs the frozen niche variation model

Lynch (1984) proposed a hypothesis that temporally variable environments select for lineages with broad ecological tolerances (general-purpose genotypes, GPG; Baker, 1965), and regards this as an important factor for geographical parthenogenesis. More recent experimental studies on parthenogenetic animals (Gade & Parker, 1997; Robinson *et al.*, 2002; Vorburger *et al.*, 2003) and apomictic plants (de Kovel & Jong, 1999) do not support the GPG hypothesis. The fact that clones are predominantly restricted to single localities indirectly contradicts the GPG hypothesis, because a general-purpose genotype

would be expected to occupy broader distribution ranges than a specialized one. Nevertheless, as the GPG hypothesis is based on temporal heterogeneity of environments, snapshot-like diversity patterns may not show the potential of maintenance of advantageous genotypes over longer time periods.

The frozen niche variation (FNV) model (Vrijenhoek, 1984, 1994) suggests that arrays of apomictic lineages are regularly produced by sexual taxa by hybridization, and each lineage 'freezes' a portion of the genotypic variation of the sexual parent. Natural selection acts on the lineages and leads to niche partitioning among lineages; single lineages have a narrower ecological niche than sexuals, but all lineages together use the resource space more effectively than sexuals (Fig. 3d).

Niche partitioning among apomicts and/or sexuals vs apomicts has been observed in many studies on asexual animals (Vrijenhoek, 1994; Jokela *et al.*, 1997; Semlitsch *et al.*, 1997; Gray & Weeks, 2001) and plants (Vavrek *et al.*, 1998; Hörandl *et al.*, 2000; Meirmans *et al.*, 2003; Verduijn *et al.*, 2004; Paun *et al.*, 2006a). Reviews of molecular population studies in plants support the importance of clonal diversity for range expansions (Gornall, 1999; Hörandl & Paun, In press). Niche differentiation may even prevent extinction of sexual reproduction, as shown by modelling the FNV model against the negative effects of accumulation of deleterious mutations in apomicts (Pound *et al.*, 2004). For geographical parthenogenesis, the findings probably suggest a higher capacity of apomicts to colonize spatially heterogeneous environments better than their sexual relatives. Avoidance of genetic load and inbreeding depression may be an important initial advantage of asexual organisms in marginal and subdivided habitats, where populations exist as 'metapopulations' with high degrees of subdivision, local extinction and recolonization (Haag & Ebert, 2004). Moderately disturbed, patchy, man-made environments, which provide novel habitats such as meadows and pastures, may thus promote range expansions of apomicts. This could be an important factor for range expansions of apomicts when they occur in same latitude/altitude as sexuals, where advantages of apomixis related to colder climates are less plausible.

The problems of the model are that (1) niche differentiation is not a general feature, because a number of genera have co-occuring sexual and apomictic taxa; and (2) the model should be effective mainly within or near the area of sympatric sexuals, where arrays of new clones are regularly produced by hybridization. Increase of clonal diversity of apomicts in sympatric areas is probably caused by backcrossing to sexuals (reviewed in Hörandl *et al.*, 2001; Hörandl & Paun, In press; Fig. 3d). But if the apomict colonizes areas distant from sexual ancestors, or if distribution areas of sexual species become separated, the only remaining sources of genotypic variation are facultative sexuality and mutations within lineages, thus drastically reducing the potential to create novel genotypes. That is, the observed extreme range expansions of apomictic complexes outside the sympatric sexual/apomictic range, and outside overlapping ranges of sexuals, are not easily explained

by the FNV model alone. Here a combination of niche differentiation *plus* uniparental reproduction for stepwise colonization offers the best explanation (Fig. 3d).

Biotic interactions – the Red Queen hypothesis

The northern tendency of apomictic complexes has often been related to a lower capacity of asexuals to keep pace with coevolving parasites and pathogens. Asexual organisms are thought to have fewer disadvantages than sexuals in environments with few biotic interactions, such as in high altitudes, high latitudes and arid habitats (Bell, 1982; Glesener & Tilman, 1987).

The expected relation of biotic interactions to geographical patterns of apomicts is not supported in regions where apomicts and sexuals coexist in the same longitudinal range, where even mixed populations may occur (see examples above). Other contradictions are the facts that, for example in Fennoscandia, the abundance of apomictic species themselves clearly increases from north to south, and in Europe is highest in the temperate zone, but decreases southwards only relative to sexual species. Moreover, frequencies of apomicts become low in extremely high latitudes and altitudes, where biotic interactions are expected to be lowest (Asker & Jerling, 1992). In the European Alps, the phanerogamic flora in the glacier regions above 4000 m includes no apomictic taxa (Ozenda, 1988).

If biotic interactions are responsible for limitation of asexual distributions, it would be expected that high pressure of predators can drive asexuals to extinction. Long-term studies over >10 yr on parthenogenetic animals and apomictic weeds suggest that parasites drive host populations through cycles, in which the most common lineages decrease and rare lineages become frequent (Burdon *et al.*, 1981; Lively & Jokela, 2002; Jokela *et al.*, 2003). Nevertheless, the Red Queen model was not supported in other long-term studies on parthenogenetic freshwater snails (Ben-Ami & Heller, 2005), and in a clonal-sexual fish complex (Weeks, 1996). Resistance against rust fungi was observed in eight of 19 phenotypes of apomictic *Chondrilla* in Turkey (Espiau *et al.*, 1998). In the grass *Miscanthus sinensis* most populations were infected by endophytic fungi, except apomictic *M. sinensis* var. *condensatus* (Chou *et al.*, 2000).

The few studies cited above suggest that predators may indeed select for genetic variation, but on the other hand none of the studies supports the idea that predators can drive asexual organisms to extinction. Once apomixis has arisen, the recombination rate, and thus the ability to adapt to predators with a short turnover of generation, is expected to decrease, but this may be overcome by maintenance of clonal diversity.

Another general caveat is needed because of a likely change of response against predators resulting from changes in composition and expression of secondary metabolites in hybrids and polyploids. Hybrids may express all the secondary chemicals of the parental taxa; may fail to express certain parental chemicals; or may express novel chemicals that are absent in each parent.

Hybridization may diversify chemical compounds, lead to introgression of resistance traits, facilitate host shifts, or act as sinks for herbivores (Orians, 2000). Differential expression and quantitative changes of metabolites have already been assessed in F_1 hybrids (Kirk *et al.*, 2005), and variation of chemical compounds tends to increase with the number of hybrid generations (Orians, 2000). From this information on sexual hybrids, it is to be expected that an apomict of hybrid origin has a different expression of chemical compounds than its sexual parents, and would also react differently to predators. Empirical studies of metabolomic profiles in apomictic plants, their response to predators, and how this could influence distribution patterns, are largely missing.

In summary, understanding of the impact of biotic interactions on geographical distributions of apomictic vs sexual plants is currently limited, and it remains uncertain whether biotic interactions are an important causal factor for geographical parthenogenesis.

Conclusion – a synthetic approach

The main conclusion of this review is that various factors contribute, to a certain extent, to geographical parthenogenesis. As discussed above, none of the factors alone is unequivocal and effective only within a certain context. Here I suggest a combination theory in a spatial and temporal context.

The tendency of apomictic plants to colonize previously glaciated areas is seen in a predominant origin of apomicts on the margins of former ice sheets, where extensive range fluctuations offered opportunities for hybridization and polyploidization. These processes probably triggered the genetic or epigenetic changes that have altered the reproductive pathway to make apomixis functional. This does not preclude origins of apomixis elsewhere, but makes the origin of apomixis in more southern regions less likely. A young age of apomictic complexes, plus a limited capacity for colonization after long-distance dispersal, restricts distribution areas mainly to their continents of origin.

In the temporal course of development, polyploidy and the hybrid nature of apomicts are important for the creation of initial basic genotypic diversity and genomic novelty. The shift to apomixis causes a strong reproductive barrier against the sexual parents, and helps to maintain and multiply apomictic lineages. In initial periods of coexistence of apomicts and sexuals, unidirectional hybridization in mixed sexual–apomictic populations may decrease frequencies of sexual individuals. During subsequent colonization of new areas and/or certain habitats, apomictic lineages may disperse more quickly than their self-incompatible sexual relatives because of uniparental reproduction. Higher initial frequencies of apomicts in new areas prevent sexual individuals from establishment. In the long run, apomicts may suffer from a lower potential to maintain and increase genetic diversity, especially in regions distant from the sexual area. Nevertheless, for the sexual relative the advantages of sexuality may be manifest too late

to compensate for the initial distributional success of apomicts.

In spatial dimensions, advantages of apomictic plants in higher latitudes/altitudes over their sexual relatives are manifold: (1) a shortening of the reproductive pathway and faster seed development in shorter vegetation periods; (2) reproductive assurance if pollinators and mating partners are rare; and (3) potentially less pressure from predators because of reduced biotic interactions from colder climates. Together with the factors above, high altitudinal/latitudinal sexual relatives may be replaced by apomicts. This combination of factors may also explain an overall increase in apomicts relative to the rest of the sexual flora in northern regions (Asker & Jerling, 1992). In temperate or more southern regions, advantages related to a colder climate are perhaps not effective enough to explain the distributional success of apomicts. Here, niche differentiation of apomicts and sexuals may help to maintain sympatric areas. Clonal diversity allows niche differentiation among lineages and optimal use of resource space by apomictic lineages. This is probably important for range expansions in spatially and temporally heterogeneous environments, and may explain the tendency to man-made habitats.

Each factor has its limitations, and can be compensated by features of sexuality. Indirectly, these conclusions may shed light on the still frequently discussed question of why sex is predominant in nature and not replaced by asexual reproduction. (1) At least in angiosperms, the shift to apomixis requires complex changes in reproductive pathways. A predisposition of certain taxa, plus an opportunity for polyploidization and/or hybridization as trigger for the required genetic or epigenetic changes, must coincide to make apomixis functional; this happens much more rarely than other modifications of the sexual system (Table 1). (2) For establishment of apomixis, the newly arisen apomict has to compete with a large pool of sexual allopolyploid lineages with features similar to the apomict: genomic novelty plus an effective reproductive isolation mechanism. (3) Uniparental reproduction and maintenance of heterozygosity offer short-term advantages for colonization of new areas, but this can be compensated by self-fertilization of sexuals, which is more frequently established in angiosperms (Table 1). Sexuals can probably re-establish genetic variation more effectively after a bottleneck, and speciate more rapidly after strong geographical isolation. Apomicts, in contrast, need longer time periods and/or multiple colonizations for the creation of clonal diversity. (4) Selfing, niche differentiation, and isolation by different ploidy levels prevent total replacement of sexuals by introgression of apomixis via pollen. Exploration of novel niches and range expansions of apomicts probably require a certain level of clonal diversity that is best maintained near the sympatric sexual area or via stepwise migration. (5) Apomictic reproduction is advantageous mainly in colder or more extreme climates and/or certain ecological conditions: heterogeneous, moderately disturbed environments. Consequently, apomicts are perhaps more successful than sexuals

because of not only a single factor, but a combination of factors acting together. This might not occur frequently enough to replace the well established and more flexible system of sexuality.

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References

Adams KL, Wendel JF. 2005. Polyploidy and genome evolution in plants. *Current Opinion in Plant Biology* **8**: 135–141.

Amsellem L, Noyer J-L, Hossaert-McKey M. 2001. Evidence for a switch in the reproductive biology of *Rubus alceifolius* (Rosaceae) towards apomixis, between its native range and its area of introduction. *American Journal of Botany* **88**: 2243–2251.

Anderson GJ, Bernardello G, Stuessy TF, Crawford DJ. 2001. Breeding system and pollination of selected plants endemic to Juan Fernández Islands. *American Journal of Botany* **88**: 220–233.

Arnold ML. 1997. *Natural Hybridization and Evolution.* Oxford, UK: Oxford University Press.

Arnold ML, Bennett BD. 1993. Natural hybridization in Louisiana Irises: genetic variation and ecological determinants. In: Harrison RG, ed. *Hybrid zones and the evolutionary process.* New York: Oxford University Press, 115–139.

Asker SE, Jerling L. 1992. *Apomixis in plants.* Boca Raton, FL, USA: CRC Press.

Baker HG. 1967. Support for Baker's law – as a rule. *Evolution* **21**: 853–856.

Baker HG. 1965. Characteristics and Modes of Origin of Weeds. In: Baker HG, Stebbins GL, eds. *The genetics of colonizing species.* New York, NY, USA: Academic Press, 147–168.

Barrett SCH. 1996. The reproductive biology and genetics of island plants. *Philosophical Transactions of the Royal Society of London B* **351**: 723–733.

Barrett SCH, Pannell JR. 1999. Metapopulation dynamics and mating system evolution in plants. In: Hollingsworth PM, Bateman RM, Gornall RJ, eds. *Molecular systematics and plant evolution.* London: Taylor & Francis, 74–100.

Battjes J, Menken SBJ, den Nijs HJCM. 1992. Clonal diversity in some microspecies of *Taraxacum* sect. *Palustria* (Lindeb. fil.) Dahlst. from Czechoslovakia. *Botanische Jahrbücher für Systematik* **114**: 315–328.

Bayer RJ. 1990. Investigations into the evolutionary history of the *Antennaria rosea* (Asteraceae: Inuleae) polyploid complex. *Plant Systematics and Evolution* **169**: 97–110.

Bayer RJ. 1991. Allozymic and morphological variation in *Antennaria* (Asteraceae: Inuleae) from the low arctic of northwestern North America. *Systematic Botany* **16**: 492–506.

Bell G. 1982. *The masterpiece of nature: the evolution and genetics of sexuality.* Berkeley, CA, USA: California Press.

Ben-Ami F, Heller J. 2005. Spatial and temporal patterns of parthenogenesis and parasitism in the freshwater snail *Melanoides tuberculata.* *Journal of Evolutionary Biology* **138**: 138–146.

Bernardello G, Anderson GJ, Stuessy TF, Cawford DJ. 2001. A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernández Islands (Chile). *Botanical Review* **67**: 255–308.

Bicknell RA, Koltunow AM. 2004. Understanding apomixis: recent advances and remaining conundrums. *Plant Cell* **16**: S228–S245.

Bierzychudek P. 1985. Patterns in plant parthenogenesis. *Experientia* **41**: 1255–1264.

Brochmann C, Gabrielsen TM, Nordal I, Landvik JY, Elven R. 2003. Glacial survival or tabula rasa? The history of North Atlantic biota revisited. *Taxon* **52**: 417–450.

Brochmann C, Brysting AK, Alsos IG, Borgen L, Grundt HH, Scheen AC, Elven R. 2004. Polyploidy in arctic plants. *Biological Journal of the Linnean Society* **82**: 521–536.

Brock MT. 2004. The potential for genetic assimilation of a native dandelion species, *Taraxacum ceratophorum* (Asteraceae), by the exotic congener *T. officinale.* *American Journal of Botany* **91**: 656–663.

Burdon JJ, Groves RH, Cullen JM. 1981. The impact of biological control on the distribution and abundance of *Chondrilla juncea* in South-Eastern Australia. *Journal of Applied Ecology* **18**: 957–966.

Burt A. 2000. Perspective: sex, recombination and the efficacy of selection – was Weismann right? *Evolution* **54**: 337–351.

Carillo C, Britton NF, Mogie M. 2002. Coexistence of sexual and asexual conspecifics: a cellular automaton model. *Journal of Theoretical Biology* **217**: 275–285.

Carino DA, Daehler CC. 1999. Genetic variation in an apomictic grass, *Heteropogon contortus*, in the Hawaiian Islands. *Molecular Ecology* **8**: 2127–2132.

Carman JG. 1997. Asynchronous expression of duplicate genes in angiosperms may cause apomixis, bispory, tetraspory, and polyembryony. *Biological Journal of the Linnean Society* **61**: 51–94.

Carman JG. 2001. The gene effect: genome collisions and apomixis. In: Savidan Y, Carman JG, Dresselhaus T, eds. *The flowering of apomixis: from mechanisms to genetic engineering.* Mexico DF: CIMMYT, 95–110.

Carr DE, Dudash MR. 2003. Recent approaches to the genetic basis of inbreeding depression in plants. *Philosophical Transactions of the Royal Society of London B* **358**: 1071–1084.

Chapman HM, Parh D, Oraguzie N. 2000. Genetic structure and colonizing success of a clonal weedy species, *Pilosella officinarum* (Asteraceae). *Heredity* **84**: 401–409.

Chou CH, Chiang YC, Chiang TY. 2000. Genetic variability and phytogeography of *Miscanthus sinensis* var. *condensatus*, an apomictic grass, based on RAPD fingerprints. *Canadian Journal of Botany* **78**: 1262–1268.

Comai L. 2005. The advantages and disadvantages of being polyploid. *Nature Reviews Genetics* **6**: 836–846.

Dobeš C, Mitchell-Olds T, Koch MA. 2004a. Extensive chloroplast haplotype variation indicates Pleistocene hybridization and radiation of North American *Arabis drummondii*, *A. × divaricarpa*, and *A. holboellii* (Brassicaceae). *Molecular Ecology* **13**: 349–370.

Dobeš C, Mitchell-Olds T, Koch MA. 2004b. Interspecific diversification in North American *Boechera stricta* (= *Arabis drummondii*), *Boechera × divaricarpa*, and *A. holboellii* (Brassicaceae) inferred from nuclear and chloroplast molecular markers – an integrative approach. *American Journal of Botany* **91**: 2087–2101.

Ericsson S. 2001. *Ranunculus auricomus* complex. In: Jonsell B, Karlsson T, eds. *Flora Nordica, Vol. 2. Chenopodiaceae to Fumariaceae.* Stockholm: Bergius Foundation, 237–255.

Espiau C, Riviere D, Burdon JJ, Gartner S, Daclinat B, Hasan S, Chaboudez P. 1998. Host–pathogen diversity in a wild system, *Chondrilla juncea–Puccinia chondrillina.* *Oecologia* **113**: 133–139.

Fehrer J, Šimek R, Krahulcová A, Krahulec F, Chrtek J, Bräutigam E, Bräutigam S. 2005. Evolution, hybridisation, and clonal distribution of apo- and amphimictic species of *Hieracium* subgen. *Pilosella* (Asteraceae, Lactuceae) in a central European mountain range. In: Bakker F, Chatrou L, Gravendeel B, Pelser PB, eds. *Plant species-level systematics: new perspectives on pattern and process.* Ruggell, Liechtenstein: Gantner Verlag, 175–201.

Fröhner S. 1990. Alchemilla. In: Conert HJ, Hamann U, Schultze-Motel W, Wagenitz G, eds. *Gustav Hegi, Illustrierte Flora Von Mitteleuropa, Vol. IV. 2b, eds. 3.* Berlin: Parey, 13–242.

Gade B, Parker ED. 1997. The effect of life cycle stage and genotype

on desiccation tolerance in the colonizing parthenogenetic cockroach *Pycnoscelus surinamensis* and its sexual ancestor *P. indicus*. *Journal of Evolutionary Biology* **10**: 479–493.

Glesener RR, Tilman D. 1987. Sexuality and the components of environmental uncertainty, clues from geographic parthenogenesis in terrestrial animals. *American Naturalist* **112**: 169–673.

Gornall RJ. 1999. Population genetic structure in agamospermous plants. In: Hollingsworth PM, Bateman RM, Gornall RJ, eds. *Molecular systematics and plant evolution*. London: Taylor & Francis, 118–138.

Grant V. 1981. *Plant speciation*, 2nd edn. New York, NY, USA: Columbia University Press.

Gray MM, Weeks SC. 2001. Niche breadth in clonal and sexual fish (*Poeciliopsis*), a test of the frozen niche variation model. *Canadian Journal of Fishery and Aquatic Sciences* **58**: 1313–1318.

Grimanelli D, Leblanc O, Perotti E, Grossniklaus U. 2001. Developmental genetics of gametophytic apomixis. *Trends in Genetics* **17**: 597–604.

Grimanelli D, Garcia M, Kaszas E, Perotti E, Leblanc O. 2003. Heterochronic expression of sexual reproductive programs during apomictic development in *Tripsacum*. *Genetics* **165**: 1521–1531.

Haag CR, Ebert D. 2004. A new hypothesis to explain geographic parthenogenesis. *Annales Zoologicae Fennicae* **41**: 539–544.

Harrison RG. 1993. Hybrids and hybrid zones: historical perspective. In: Harrison RG, ed. *Hybrid zones and the evolutionary process*. Oxford, UK: Oxford University Press, 3–12.

Heenan PB, Dawson MI, Bicknell RA. 2002. Evidence for apomictic seed formation in *Coprosma waima* (Rubiaceae). *New Zealand Journal of Botany* **40**: 347–355.

Heenan PB, Molloy BPJ, Bicknell RA, Luo C. 2003. Levels of apomictic and amphimictic seed formation in a natural population of *Coprosma robusta* (Rubiaceae) in Riccarton Bush, Christchurch, New Zealand. *New Zealand Journal of Botany* **41**: 287–291.

Holsinger KE. 2000. Reproductive systems and evolution in vascular plants. *Proceedings of the Natural Academy of Sciences, USA* **97**: 7037–7042.

Hörandl E, Greilhuber J. 2002. Diploid and autotetraploid sexuals and their relationships to apomicts in the *Ranunculus cassubicus* group: insights from DNA content and isozyme variation. *Plant Systematics and Evolution* **234**: 85–100.

Hörandl E, Paun O. In press. Patterns and sources of genetic diversity in apomictic plants: implications for evolutionary potentials and ecology. In: Hörandl E, Grossniklaus U, Sharbel T, van Dijk P, eds. *Apomixis: Evolution, Mechanisms and Perspectives*. Ruggell, Liechtenstein: Gantner Verlag. (In press.)

Hörandl E, Greilhuber J, Dobes C. 2000. Isozyme variation and ploidy levels within the apomictic *Ranunculus auricomus* complex: evidence for a sexual progenitor species in southeastern Austria. *Plant Biology* **2**: 53–62.

Hörandl E, Jakubowsky G, Dobeš Ch. 2001. Isozyme and morphological diversity within apomictic and sexual taxa of the *Ranunculus auricomus* complex. *Plant Systematics and Evolution* **226**: 165–185.

Houliston GJ, Chapman HM. 2004. Reproductive strategy and population variability in the facultative apomict *Hieracium pilosella* (Asteraceae). *American Journal of Botany* **91**: 37–44.

Jokela J, Lively CM, Fox JA, Dybdahl MF. 1997. Flat reaction norms and 'frozen' phenotypic variation in clonal snails (*Potamopyrgus antipodarum*). *Evolution* **51**: 1120–1129.

Jokela J, Lively CM, Dybdahl MF, Fox JA. 2003. Genetic variation in sexual and clonal lineages of a freshwater snail. *Biological Journal of the Linnean Society* **79**: 165–181.

Jonsell B, Karlsson T. 2004. Endemic vascular plants in Norden. In: Jonsell B, ed. *Flora Nordica, General Volume*. Stockholm: Bergius Foundation, 139–159.

Kearney M. 2005. Hybridization, glaciation and geographical parthenogenesis. *Trends in Ecology and Evolution* **20**: 495–502.

Kirk H, Choi YH, Kim HK, Verpoorte R, van der Meijden E. 2005. Comparing metabolomes: the chemical consequences of hybridization in plants. *New Phytologist* **167**: 613–622.

Kollmann J, Steinger T, Roy BR. 2000. Evidence of sexuality in European *Rubus* (Rosaceae) species based on AFLP and allozyme analysis. *American Journal of Botany* **87**: 1592–1598.

Koltunow A, Grossniklaus U. 2003. Apomixis, a developmental perspective. *Annual Review of Plant Biology* **54**: 547–574.

de Kovel CGF, Jong G. 1999. Responses of sexual and apomictic genotypes of *Taraxacum officinale* to variation in light. *Plant Biology* **1**: 541–546.

Kraft T, Nybom H, Werlemark G. 1996. DNA fingerprint variation in some blackberry species (*Rubus* subg. *Rubus*, Rosaceae). *Plant Systematics and Evolution* **199**: 93–108.

Krahulcova A, Chrtek J, Krahulec F. 1999. Autogamy in *Hieracium* subgen. *pilosella*. *Folia Geobotanica* **34**: 373–376.

Levin DA. 2002. *The Role of Chromosome Change in Plant Evolution*. Oxford, UK: Oxford University Press.

Lively CM, Jokela J. 2002. Temporal and spatial distributions of parasites and sex in a freshwater snail. *Evolutionary and Ecological Research* **4**: 219–226.

Lynch M. 1984. Destabilizing hybridization, general-purpose genotypes and geographic parthenogenesis. *Quarterly Review of Biology* **59**: 257–290.

Marble BK. 2004. Polyploidy and self-compatibility: is there an association? *New Phytologist* **162**: 803–811.

Matzk F, Prodanovic S, Bäumlein H, Schubert I. 2005. The inheritance of apomixis in *Poa pratensis* confirms a five locus model with differences in gene expressivity and penetrance. *Plant Cell* **17**: 13–24.

Maynard Smith J. 1978. *The Evolution of Sex*. Cambridge, UK: Cambridge University Press.

Meirmans PG, Vlot EC, Den Nijs JCM, Menken SBJ. 2003. Spatial ecological and genetic structure of a mixed population of sexual diploid and apomictic triploid dandelions. *Journal of Evolutionary Biology* **16**: 343–352.

Meirmans PG, Den Nijs JCM, Van Tienderen PH. 2006. Male sterility in triploid dandelions: asexual females vs asexual hermaphrodites. *Heredity* **96**: 45–52.

Mogie M. 1992. *The evolution of asexual reproduction in plants*. London: Chapman & Hall.

Mogie M, Britton NF, Stewart-Cox JA. In press. Asexuality, polyploidy and the male function. In: Hörandl E, Grossniklaus U, Sharbel T, van Dijk P, eds. *Apomixis, evolution, mechanisms and perspectives*. Ruggell, Liechtenstein: Gantner Verlag. (In press.)

Morita T, Menken SBJ, Sterk AA. 1990. Hybridization between European and Asian dandelions (*Taraxacum* section *Ruderalia* and section *Mongolica*). 1. Crossability and breakdown of self-incompatibility. *New Phytologist* **114**: 519–529.

Nybom H. 1986. Active self-pollination in blackberries (*Rubus* subgen. *Rubus*, Rosaceae). *Nordic Journal of Botany* **5**: 521–525.

Orians CM. 2000. The effects of hybridization in plants on secondary chemistry: implications for the ecology and evolution of plant–herbivore interactions. *American Journal of Botany* **87**: 1749–1756.

Ozenda P. 1988. *Die vegetation der Alpen im Europäischen Gebirgsraum*. Stuttgart, Germany: Gustav Fischer Verlag.

Palacios C, Gonzalez-Candelas F. 1997. Analysis of population genetic structure and variability using RAPD markers in the endemic and endangered *Limonium dufourii* (Plumbaginaceae). *Molecular Ecology* **6**: 1107–1121.

Paun O, Greilhuber J, Temsch E, Hörandl E. 2006a. Patterns, sources and ecological implications of clonal diversity in apomictic *Ranunculus carpaticola* (*Ranunculus auricomus* complex, Ranunculaceae). *Molecular Ecology* **15**: 897–910.

Paun O, Stuessy TF, Hörandl E. 2006b. The role of hybridization, polyploidization and glaciation for the origin and evolution of the apomictic *Ranunculus cassubicus* complex. *New Phytologist* **171**: 223–236.

Peck JR, Yearsley JM, Waxman D. 1998. Explaining the geographic distributions of sexual and asexual populations. *Nature* **391**: 889–892.

Pound GE, Cox SJ, Doncaster CP. 2004. The accumulation of deleterious mutations within the frozen niche variation hypothesis. *Journal of Evolutionary Biology* **17**: 651–662.

Quarin CL, Espinoza F, Martinez EJ, Pessino SC, Bovo OA. 2001. A rise of ploidy level induces the expression of apomixis in *Paspalum notatum*. *Sexual Plant Reproduction* **13**: 243–249.

Ramsey J, Schemske DW. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics* **29**: 467–501.

Rapp RA, Wendel JF. 2005. Epigenetics and plant evolution. *New Phytologist* **168**: 81–91.

Richards AJ. 1997. *Plant breeding*. London: Chapman & Hall.

Richards AJ. 2003. Apomixis in flowering plants: an overview. *Philosophical Transactions of the Royal Society of London B* **358**: 1085–1093.

Rieseberg LH, Wendel JF. 1993. Introgression and its consequences in plants. In: Harrison RG, ed. *hybrid zones and the evolutionary process.* Oxford, UK: Oxford University Press, 70–109.

Rieseberg LH, Raymond O, Rosenthal DM, Lai Z, Livingstone K, Nakazato T, Durphy J, Schwarzbach AE, Donovan LA, Lexer C. 2003. Major ecological transitions in wild sunflowers facilitated by hybridization. *Science* **301**: 1211–1216.

Robinson MT, Weeks AR, Hoffmann AA. 2002. Geographic patterns of clonal diversity in the earth mite species *Penthaleus major* with particular emphasis on species margins. *Evolution* **56**: 1160–1167.

Rutishauser A. 1954. Die Entwicklungserregung des Endosperms bei pseudogamen Ranunculusarten. *Mitteilungen der Naturforschenden Gesellschaft Schaffhausen* **25**: 1–45.

Savidan Y, Carman JG, Dresselhaus T. 2001. *The flowering of apomixis: from mechanisms to genetic engineering*. Mexico DF: CIMMYT.

Seehausen O. 2004. Hybridization and adaptive radiation. *Trends in Ecology and Evolution* **19**: 198–207.

Semlitsch RD, Hotz H, Guex GD. 1997. Competition among tadpoles of coexisting hemiclones of hybridogenetic *Rana esculenta*: support for the Frozen Niche Variation model. *Evolution* **51**: 1249–1261.

Sharbel TF, Mitchell-Olds T. 2001. Recurrent polyploid origins and chloroplast phylogeography in the *Arabis holboellii* complex (Brasicaceae). *Heredity* **87**: 59–68.

Soejima A, Yahara T, Watanabe K. 2001. Distribution and variation of sexual and agamospermous populations of *Stevia* (Asteraceae: Eupatorieae) in lower latitudes, Mexico. *Plant Species Biology* **16**: 91–105.

Spielmann M, Vinkenoog R, Scott RJ. 2003. Genetic mechanisms of apomixis. *Philosophical Transactions of the Royal Society of London B* **358**: 1095–1103.

Stace C. 1976. *Hybridization and the flora of the British Islands*. New York: Academic Press.

Stebbins GL. 1950. *Variation and evolution in plants*. New York: Columbia University Press.

Stebbins GL, Dawe JC. 1987. Polyploidy and distribution in the European flora: a reappraisal. *Botanische Jahrbücher für Systematik* **108**: 343–354.

Stuessy TF, Jakubowsky G, Salguero Gómez R, Pfosser M, Schlüter PM, Fer T, Sun B-Y, Kato H. 2006. Anagenetic evolution in island plants. *Journal of Biogeography*. (In press.)

Tas ICQ, Van Dijk P. 1999. Crosses between sexual and apomictic dandelions (*Taraxacum*). I. The inheritance of apomixis. *Heredity* **83**: 707–714.

Trewick SA, Morgan-Richards M, Chapman HM. 2004. Chloroplast DNA diversity of *Hieracium pilosella* (Asteraceae) introduced to New Zealand,

reticulation, hybridization, and invasion. *American Journal of Botany* **91**: 73–85.

Tyler T. 2000. Detecting migration routes and barriers by examining the distribution of species in an apomictic species complex. *Journal of Biogeography* **27**: 979–988.

Urbani MH. 2002. Cytogeography and reproduction of the *Paspalum simplex* polyploid complex. *Plant Systematics and Evolution* **236**: 99–105.

Van Der Hulst RGM, Mes THM, den Nijs JCM, Bachmann K. 2000. Amplified fragment length polymorphism reveal that population structure of triploid dandelions (*Taraxacum officinale*) exhibits both clonality and recombination. *Molecular Ecology* **9**: 1–8.

Van Dijk P. 2003. Ecological and evolutionary opportunities of apomixis: insights from *Taraxacum* and *Chondrilla*. *Philosophical Transactions of the Royal Society of London B* **358**: 1113–1121.

Van Dijk PJ, Vijverberg K. 2005. The significance of apomixis in the evolution of the angiosperms: a reappraisal. In: Bakker F, Chatrou L, Gravendeel B, Pelser PB, eds. *Plant species-level systematics: new perspectives on pattern and process.* Ruggell, Liechtenstein: Gantner Verlag, 101–116.

Vandel A. 1928. La parthénogenese geographique. Contribution a l'étude biologique de la parthénogenese naturelle. *Bulletin Biologique de la France et de la Belgique* **62**: 164–182.

Vavrek JMC, McGraw JB, Yang HS. 1998. Within-population variation in demography of *Taraxacum officinale* (Asteraceae): differential genotype response and effect on interspecific competition. *American Journal of Botany* **85**: 947–954.

Verduijn MH, Van Dijk P, van Damme JMM. 2004. Distribution, phenology and demography of sympatric sexual and asexual dandelions (*Taraxacum officinale* s.l.): geographical parthenogenesis on small scale. *Biological Journal of the Linnean Society* **82**: 205–218.

Vorburger C, Sunnucks P, Ward SA. 2003. Explaining the coexistence of asexuals with their sexual progenitors: no evidence for general-purpose genotypes in obligate parthenogens of the peach-potato aphid, *Myzus persicae*. *Ecology Letters* **6**: 1091–1098.

Vrijenhoek RC. 1984. Ecological differentiation among clones: the frozen niche variation model. In: Woermann K, Loeschcke V, eds. *Population biology and evolution.* Berlin: Springer, 217–231.

Vrijenhoek RC. 1994. Unisexual fish: model systems for studying ecology and evolution. *Annual Review of Ecology and Systematics* **25**: 71–96.

Weber HE. 1995. *Rubus*. In: Conert H J, Hamann U, Schultze-Motel W, Wagenitz G, eds. *Gustav Hegi, Illustrierte Flora von Mitteleuropa, vol. IV. 2a, eds. 3.* München, Germany: Parey, 284–595.

Weeks SC. 1996. A reevaluation of the Red Queen model for the maintenance of sex in a clonal-sexual fish complex (Poeciliidae: *Poeciliopsis*). *Canadian Journal of Fishery and Aquatic Sciences* **53**: 1157–1164.

Wolfe AD, Qiang QY, Kepharts SR. 1998a. Diploid hybrid speciation in *Penstemon* (Scrophulariaceae). *Proceedings of the Natural Academy of Sciences, USA* **95**: 5112–5115.

Wolfe AD, Qiang QY, Kepharts SR. 1998b. Assessing hybridization in natural populations of *Penstemon* (Scrophulariaceae) using hypervariable intersimple sequence repeat (ISSR) bands. *Molecular Ecology* **7**: 1107–1125.

Yahara T. 1990. Evolution of agamospermous races in *Boehmeria* and *Eupatorium*. *Plant Species Biology* **5**: 183–196.

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