Narrow roads to Fern Land:
Revisiting and re-analysing the paradox of sexual reproduction

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Abstract. Some major thought on the evolutionary maintenance of sexual reproduction is revisited. This leads to a new perspective about the role of complex life cycles for the maintenance of sex. And it leads to a new comparison of organisms with different life cycles. Organisms like strawberries propagate contrary to what would be adaptive under red-queen selection from micro-parasites. Their recombinant offspring disperses, and their clonal offspring stays close to the parent. In organisms like ferns fertilisation and meiosis occur in different generations. Their zygotes grow on the spot of their maternal gametophyte and are recombinant through syngamy. The resulting sporophytes produce dispersing spores, which are also recombinant through meiosis. This should better adapt ferns to red-queen selection than strawberries or corals. Hence, ferns are a good reference group to strawberry like organisms.

We tested fungal parasite richness of ferns against that of strawberry like plants, (strawberries & cinquefoils). The occurrence and number of fungi was significantly higher in the strawberry-like plants. This refutes the hypothesis that organisms like strawberries falsify the red-queen model. They would do better with recombinant offspring that stays, and clonal offspring that disperses. Yet, this would amount to sexually producing runners, tubers, polyps, etc. This may well-nigh be an evolutionary impossibility. Theoretically, life cycles with recombinant offspring that stay and clonal offspring that disperse should be best adapted against red-queen selection from micro-parasites. The rarity of this "red-queen life cycle" among multicellular species remains perplexing.

Key Words: diplontic, haplontic, heterogonic, diplohaplontic, parasite species richness, strawberry-coral model, red-queen model, fern species, *Fragaria* L. & *Potentilla* L.

1. A narrow road from the paradox of sex to Fern Land

1.1 Cost of sexual reproduction

John Maynard Smith provided an analysis of the cost of sexual reproduction as early as 1958. It occurred within his popular science book *The Theory of Evolution*. A contribution to the *Pelican Biology Series* of paperbacks published by *Penguin Books*. Here, Maynard Smith clearly attributed the twofold cost of sex to males:

> 'If the rate of increase of an animal population were limited by the number of eggs which each female could lay, which in turn depended on how much food a female could eat and transform into eggs, then a population consisting entirely of parthenogenetic females would increase twice as fast as would a population of equal numbers of males and females. From the point of view of reproduction, males are a waste of living material. (This argument does not hold for hermaphroditic organisms, or for those animals in which both parents help to feed the young.' (Maynard Smith 1958, 138)

Michael T. Ghiselin first learned about the cost of sex through a peer review of one of his papers (Ghiselin 1969). George C. Williams happened to be that reviewer, and his source happened to be the second edition of Maynard Smith's Penguin book. But Williams already attributed the cost of sex to the genome reduction in meiosis.

> 'Williams, who reviewed the paper for the journal in which it appeared, responded by drawing attention to a point that both of them [Williams and Ghiselin] had overlooked, but that had come to his attention from a book by Maynard Smith (1966): that mictic females pass on half as many genes to the next generation as parthenogenetic females do.' (Ghiselin 1988, 16; see also Williams 1996, xii)

This difference between Maynard Smith and Williams remained constant. Maynard Smith conceived it a cost wasted on males (Maynard Smith 1971, 170-2; 1978, 3), Williams as a cost incurred through meiosis and syngamy (Williams 1971, 13; Williams and Mitton 1973; Williams 1975, 9; 1980, 373; 1988, 294).

1.2 Maintenance of sexual reproduction

They also differed in the arena for asexual and sexual reproduction to compete. Maynard Smith's point of departure were *diplontic* animal species (see fig. 1) with anisogamous haploid gametes and no paternal brood care (Maynard Smith 1958, 138; 1971, 170; 1976; 1978, 3). A mutation for asexual reproduction will genetically isolate the mutant by default.

Williams also started from diplontic species but assumed that asexual and sexual reproduction coexisted in the life cycle. (We will henceforth refer to life cycles integrating both modes of reproduction as *heterogonic*.) In heterogonic species, the allocation of resources to the modes of reproduction can gradually shift. Mutations for more asexual reproduction will not isolate the mutant from the population (Williams and Mitton 1973; Williams 1975). According to Williams (1975, 10f), an immediate benefit must balance the cost of sex in this stable coexistence with asexuality.

> 'There is no escaping the conclusion that these life cycles must be close to evolutionary equilibrium. The observed incidence of asexual and sexual reproduction must represent for these forms the currently adaptive optimum maintained by selection. In these populations there can be no net disadvantage to sexual reproduction.' (Williams 1975, 11)

Williams (1975) considered a series of model life cycles that differed in their balance of asex vs sex. The *Aphid-Rotifer* model comprised species switching between modes of reproduction at certain times. The *Strawberry-Coral* model switched to sex when the offspring would disperse in space (not time). By the way, Bell (1982) has shown that the life cycles of coelenterates (including corals) are far more diverse than being heterogonic with recombinant propagules that disperse and clonal ones that stay.

> 'In the diversity and mutability of their reproductive habits, the coelenterates have a claim to be the most protean of metazoans.' (Bell 1982, 186)

Anyway, Williams (1975) arrived at organisms with no asexual reproduction. Here, the evolutionary trade-off seemed to lie at zero investment in asexual reproduction. The *Elm-Oyster* model comprised such species with a high fecundity. Their average adult females had more than a million offspring per lifetime (zygote-to-zygote-increase: ZZI > 10^6). Williams found arguments why high fecundity species should not invest in asexual reproduction (Williams and Mitton 1973; Williams 1975, ch. 4-6). Yet he failed to do so for low fecundity species (ZZI < 10^3) such as mammals, birds, and many insects:

> 'Their present exclusive reliance on sexual reproduction must be ascribed to inheritance from a high-fecundity ancestor in which the complete replacement of asexual with sexual reproduction was the evolutionary equilibrium. If and when any form of asexual reproduction becomes feasible in higher vertebrates, it completely replaces sexual. So in these forms sexuality is a maladaptive feature, dating form a piscine of even protochordate ancestor, for which they lack the preadaptation for ridding themselves.' (Williams 1975, 102f)

Maynard Smith (1976, 254) corroborated that the maintenance of sexual reproduction required a high fecundity. Therefore, William D. Hamilton sought an immediate advantage to sex in low-fecundity species.

> 'Williams himself seems to have despaired of showing advantage for sexuality for low fecundity organisms and concludes, in effect, that most practice sex because they haven't found suitable tricks for eliminating it yet (can he really believe this for so many vertebrates?).' (Hamilton 1996 [1975], 365)
> 'My striving to find models that could cope with low fecundity as well as with twofold cost is apparent in all my sex models' (Hamilton 2001, 17)

1.3 Red-queen selection by micro-parasites

'"A slow sort of country!" said the Queen. "Now, here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!"' (Lewis Carroll: Through the Looking-Glass)

Sexual recombination will only benefit individuals, when the heritability of fitness is negative. This means that genotypes of high fittest in one generation will be of low fitness in the next. Bell (1982, 106) called this selection *capricious* in contrast to merely changeable or unpredictable selection.

Hamilton's models included capricious selection through pathogens and small parasites. Due to their shorter life cycles, they should outpace their hosts in the evolutionary race. These micro-parasites can overcome the defense mechanisms of hosts that clone themselves. They reduce their fitness more than that of hosts reproducing sexually. Hamilton's models showed that micro-parasites could cause negative heritability of fitness. That is, they could favour sexual reproduction in the short run (Hamilton, Axelrod, and Tanese 1990; Hamilton 2001).

Hamilton departed from organisms with low fecundity (e.g., mammals, birds, and scarabs). Williams' failure to account for the exclusive sexual reproduction these species

motivated him. He never modelled life cycles including both asexual and sexual reproduction. When expanding from one to many loci, Hamilton switched from diploid to haploid hosts (Hamilton 1980, 286; Hamilton, Axelrod, and Tanese 1990, 3567). [This implies haplontic rather than diplontic life cycles (see fig. 1), with negligible selection in the unicellular stages.] Hamilton took this decision for the ease of modelling (Hamilton 2001, 53), but also for avoiding mere Mendelian allele-swapping (Hamilton 2001, 611). A majority of empirical studies supported this *Red Queen* hypothesis, but a good third did not (Tobler and Schlupp 2008).

1.4 A belated challenge of C.G. Williams to the late W.D. Hamilton

Hamilton died unexpectedly in March 2000. Williams could, unfortunately, only pose his last challenge to his friend in a talk at a memorial session for Hamilton (Trivers 2015, 195). The challenge got on record in an obituary made from that talk:

> 'I am not convinced that adaptation by local pathogens to parental genotypes need be the major problem solved by sexuality. I think that the general unpredictability of offspring environments is what provides the main advantage. This issue is most appropriately settled not by modeling or data gathering but by consulting authorities. For a reliable insight on the significance of sexuality there are many appropriate authorities, but one that is especially clear is the strawberry plant (Fragaria). Offspring that develop immediately in the parents' environment, with pathogens adapted to those parents' genotypes, will not be sexually produced; whereas those that develop at variable times in the future, over a large range of habitats will be. The allocation of resources to sexual and asexual reproduction must be that which balances the two-fold cost of meiosis by the advantage of genetic diversity among widely dispersed seeds.' (Williams 2000)

The strawberry was Williams' model for a heterogonic life cycle with clonal propagules that stay, again. It either excludes the parasite Red Queen from a huge realm of life history (Dagg 2017, 58f), or that life cycle may not be optimal against micro-parasites. Unfortunately, nobody has risen to that challenge yet (but see part 2). Either way, the life cycle context is crucial for the maintenance of sexual reproduction. Life cycles that separate meiosis and male functions (fertilisation) developmentally should be particularly instructive.

1.5 Increasing life-cycle complexity to decrease perplexity

Diplontic life cycles are not ideal for parsing the cost of meiosis from that of males or fertilization (syngamy). Meiosis results in haploid gametes that fuse to form zygotes (fig. 1). That is, the processes of meiosis and syngamy (fertilization) are close to each other in development, if not in time. [Mammalian eggs do rest in the prophase of meiosis I for long times, but do not develop during this arrest.] Haplontic life cycles are neither. Here, syngamy results in a zygote that undergoes meiosis directly. Again, the syngamy and meiosis occur close to each other developmentally. Diplohaplontic life cycles alternate between generations (fig. 1). A diploid, multicellular stage produces haploid spores through meiosis, and a haploid multicellular stage produces haploid gametes trough mitosis. Syngamy and meiosis can occur at developmental antipodes of this life cycle. Strictly speaking, flowering plants are diplohaplontic (Coelho et al. 2007). The haploid stage is reduced, however, to a few cells in the

pollen grain or embryo sac. This reduction of the haploid stage puts the processes of meiosis and fertilisation close to each other. We, therefore, lump strawberries with diplontic organisms, despite the existence of a reduced haploid stage.

The haploid multicellular stage is called *gametophyte*, because it produces gametes through mitosis. Gametes are clonal to their parent gametophytes, but the zygotes are recombinant trough syngamy. The diploid, multicellular stage is called the *sporophyte*, because it produces spores through meiosis. This leads to haploid spores that are recombinant through the independent assortment of non-homologous chromosomes and crossing-over between homologous chromosomes. The haploid gametophytes can be female, male, or hermaphrodite.

To compare organisms with this life cycle with strawberries, we looked for terrestrial, perennial, and herbaceous plants. Such organisms with almost independent generations of sporophytes and gametophytes are the *Pteridophytes*. This is a paraphyletic group including ferns (monilophytes) and lycophytes (Cordle et al. 2010).

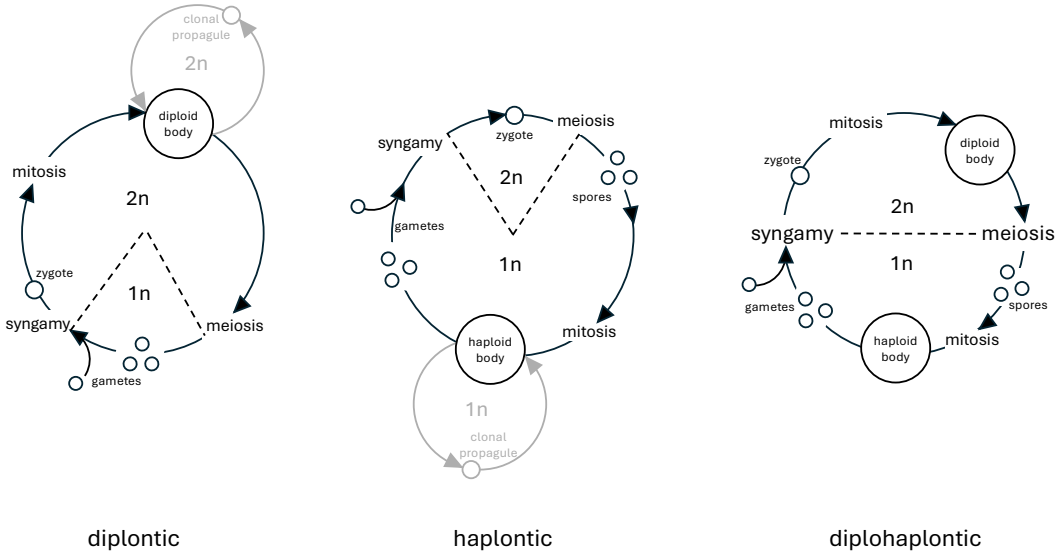

Figure 1: Life cycles.

Diplontic: The multicellular stage is diploid and produces haploid gametes that fuse directly to produce diploid zygotes. The heterogonic variant of this life cycle includes a peripheral cycle of diploid bodies producing clonal offspring (shown in grey). Maynard Smith started from the simple diplontic life cycle, where asexual mutants are genetically isolated by default. Williams started from heterogonic life cycles, where mutations that increased or decreased the amount of asexual reproduction were alleles of the same population.

Haplontic: The multicellular stage is haploid and produces gametes that fuse to produce zygotes. They undergo meiosis directly to produce haploid spores. The heterogonic variant of a haplontic life cycle includes a peripheral cycle of haploid bodies producing clonal offspring (shown in grey).

Diplohaplontic: Multicellular diploid and haploid generations occur. The diploid generation (*sporophyte*) produces recombinant spores through meiosis. These grow into the haploid generation (*gametophyte*) producing gametes through mitosis. The latter fuse to produce recombinant zygotes through syngamy. Syngamy (fertilisation) and meiosis form developmental antipodes. Heterogonic variants (not shown) could include peripheral cycles as shown in the diplontic and haplontic cycles. The diploid side-cycle does, however, lead into ploidy series in ferns, because the resulting gametophytes produce diploid gametes that fuse etc. [An asexual main cycle exists in ferns, with diploid gametophytes reproducing vegetatively (through gemmae) and diploid sporophytes producing diploid spores through *premeiotic endomitosis* or *first division restitution* (see below). That main cycle is not heterogamic however but obligate. That is, it is genetically isolated from the sexual cycle shown.]

2. Exploring Fern Land quantitatively

2.1 Introduction: a cost of asexual (not sexual) reproduction

In a diplohaplontic life cycle, haploid bodies will produce haploid gametes that fuse. There will be no cost of sex (sensu Williams 1971; 1975, 9), here, because the relatedness between haploid parent and diploid zygote will be r = 1. (The reverse will not be true. The relatedness of a diploid zygote with each haploid parent will be r = 0.5.)

If the gametes are of equal size (in equal numbers), there will be no cost of males (sensu Maynard Smith 1958, 138; 1978, 3) either. Gametes failing to find each other will lead to a high loss in unfertilized gametes. In this situation, an evolutionary process can lead to anisogamy. Disruptive selection will produce big gametes provisioning zygotes and small mobile ones (Parker, Baker, and Smith 1972; J. Lehtonen and Kokko 2011). Male gametes will get smaller and more numerous, female gametes will get bigger. This will maximize egg fertilization, though male gametes will die in great numbers. Yet, this will raise the cost of males sensu Maynard Smith. An asexual mutant could allocate the investment in male gametes to parthenogenetic ones.

However, this parthenogenetic asexuality is not found in pteridophytes for some reason (Mogie 1992, 95). Instead, the gametophyte can produce an embryo by apogamy from vegetative tissue (Grusz 2016; Hörandl 2024). Whether this asexual propagation costs more than sexual reproduction seems difficult to determine. Such an offspring could either grow autotrophic, through parental investment, or both. Experimental conditions can induce apogamy of haploid gametophytes (Cordle et al. 2010). Since the resulting sporophytes are haploid, they cannot produce spores. Therefore, natural apogamy of gametophytes comes with costly diploid propagules by sporophytes.

Diploid spores can result from two processes: first division restitution (FDR) or premeiotic endomitosis (PEM). FDR occurs when meiosis fails to separate homologous chromosomes. PEM occurs when mitosis fails to divide the nucleus and the cell. The resulting tetraploid cell undergoes meiosis. Both processes lead to diploid spores. These are twice as big but half as many as the haploid spores resulting from normal meiosis (fig. 2). Unless spore-size matters more than spore-number, a cost of meiosis (Williams 1971; Williams and Mitton 1973; Williams 1975, 9) does not occur. when reduced spores will grow into twice as many gametophytes. Then, twice as many haploid spores (r = 0.5 with sporophyte) will be equal to the diploid (r = 1 with sporophyte) ones.

The cost or benefit of meiosis depends on the advantage of propagule size vs. number (Mogie 1990; 1992, 43; 2013). The costs and benefits over the whole life cycle could roughly balance each other. Only if the advantages of size evened out that of number, would an overall benefit of apogamy remain. This trade-off between size and number should also apply to vegetative propagules (*apospory*). Yet, drawing the boundary between parental investment and propagule autotrophy should be difficult. Since apospory results in gametophytes producing diploid gametes, however, it leads into polyploidy series (Asker and Jerling 1992, 44; Mogie 1992, 61; Cordle et al. 2010). It seems to be an irrelevant alternative, then, to FDR or PEM combined with apogamy. Despite these costs of asexuality it is more frequent in ferns than any other groups of plants (Walker 1966, 155; 1985; Grusz 2016).

Ferns are also instructive about Williams' last challenge to Hamilton (see section 1.4). The sporophytes grow on the spot of their parent gametophytes, and they are recombinant. [So are the dispersing haploid spores.] If Williams challenge was correct, ferns and strawberries should be equally parasitized. Alternatively, the life cycle of ferns should render them less vulnerable to micro-parasites. Three studies are noteworthy in this respect. The first suggests fern extinction is due to physical (not biological) perturbations (S. Lehtonen et al. 2017). The other two studies suggest that ferns harbour fewer fungal pathogens than forbs (Helfer 2006; Antonovics 2020). Here, we fuse this finding to Williams' last challenge to the parasite red-queen theory (see section 1.4).

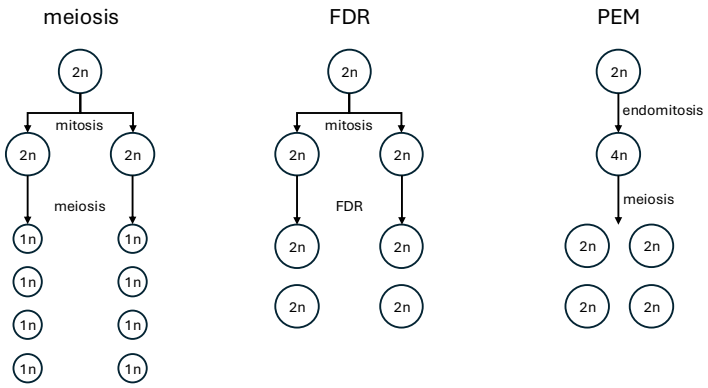

Figure 2: Simplified comparison of meiosis with first division restitution (FDR) and premeiotic endomitosis (PEM) in a diplohaplontic life cycle. Meiosis produces twice as many spores that will be half as big and related (r = 0.5). The true sequences of cell proliferation yield multiples of the above.
Normal proliferation: 4 mitoses yield 16 spore mother cells (2n) + meiosis yields 64 spores (n).
FDR Proliferation: 4 mitoses yield 16 spore mother cells (2n) + FDR meiosis yields 32 diplo-spores (2n).
PEM proliferation: 3 mitoses & 1 PEM yield 8 spore mother cells (4n) + meiosis yields 32 diplo-spores (2n).

2.2. Materials & methods

We used *The PLANTS Database* (USDA, NRCS 2024) to retrieve lists of strawberry like and fern species and the *Fungal Databases* (USDA, ARS 2024) to identify fungal species that have been recorded on the respective species. The strawberry list was retrieved by searching for "Fragaria" and setting the filters to "perennial" and "forb/herb". The USDA Plants Database retrieves *Duchesnea indica* (Andrews) Teschem., whether searching for "Fragaria" or "Potentilla". We listed it with strawberries because its berries are edible, though the genus seem to stand closer to *Potentilla* L. than *Fragaria* L. Since we pooled the strawberries and cinquefoils anyway, this taxonomic faux pas does not matter. The fern list was retrieved by setting the filters to "fern", "perennial", and "forb/herb".

Synonyms were excluded from the plant lists to minimize pseudo-replication. Varieties and subspecies were excluded for the same reason, because the *USDA Fungal Databases* also yields fungi recorded on varieties and subspecies for searches of binomial (*Genus species*) names as hosts. The "x" signifying a hybrid origin in botanical species binomials was excluded, because the USDA Fungal Database only identifies these species, when the "x" is dropped.

Because this procedure left only seven strawberry species on the *Fragaria* list, we added the closely related cinquefoils (*Potentilla* L. spp. & *Dasiphora fruticosa*). They have the same life cycle, can propagate by runners but have dry fruits. This resulted in a list of 84 strawberry-like species. The list of ferns comprised 939 species, of which 200 were chosen at random.

We used Google Scholar to estimate the study effort for each plant species. Each species binomial was entered in quotation marks and the number of search results was noted for each species. A few species had zero citations even though listed in the USDA database.

The plant species binomials were entered as host-species in the Fungal Databases without applying filters. To avoid pseudo-replication, entries of the type 'Genus sp.' and 'Genus species var. variety' were discounted, when a simple binomial (Genus species) of that taxon was also recorded. When only a variety or only a 'Genus sp.' entry of a taxon was recorded, it was counted as a datapoint. Multiple records of the same fungus from different countries were counted as only one datapoint.

We used the *R* package (R Core Team, 2018) for the statistical analysis. A logistic regression estimated whether the frequency with which at least one fungal parasite was recorded on a plant species depended on the study effort. The number of fungi recorded on a plant species was transformed into presence (1) or absence (0) of any fungi as the response variable and the number of citations (x) transformed to $\log_{10}(x+1)$ as explanatory variable. A multiple regression tested whether the plant-type was also an explanatory variable for number presence or absence of fungi recorded for a plant species using the model: (absence/presence of fungi) ~ (plant-type) + (log#citations+1).

A general linear model (glm) tested whether the number of citations (log x+1) depended on the plant-type), with a binomial link: glm(fungi(yes/no) ~ log x+1 * plant-type), where type = strawberry-like (0) or fern (1). A linear logistic regression fit was used to predict the probability of fungal records for host plants. These predictions were compared with observed probabilities calculated for number of citations grouped into classes of 0-0.5 etc. on a $\log_{10}$ scale. The number of species with any record in each class was divided by the sum of species in that class. This ratio was taken as the observed probability for that class (fig 3).

Though the interaction term of the glm was not significant (see above), the slopes differed visibly. We therefore applied the interaction model to only those host species, where one or more fungal parasites had been recorded (45 strawberry-like and 37 fern species). Since there were no zero values in this case, numbers for fungi were $\log_{10}(y)$ transformed and number of citations $\log_{10}(x)$. While this rendered the interaction term significant, it seemed possible that this was due to higher research effort expended on the agronomically important strawberries among the strawberry-like plants (strawberries + cinquefoils). Therefore, the same model was also applied to the data set excluding the five strawberries with fungal records from the 45 strawberry-like plants with fungal records.

2.3 Results

The logistic regression of detecting a fungal parasite (yes/no) on any host plant increased significantly ($P < 0.0001$) with the number of citations ($\log_{10}(x+1)$) of that host. The interaction term in the logistic regression was not significant ($p = 0.3603$) indicating no difference between ferns and strawberry-like plants in the slopes of the regressions on a logistic scale. Fungi were recorded as occurring significantly less frequently ($P < 0.0001$) on fern species than strawberry-like species after controlling for the search effort on each plant species (Fig. 3). The difference in means of the logistic regression was 0.195 (95% confidence intervals -0.764–0.426). Inspecting figure 3 helps to interpret this result. At citation numbers of 100 (2 on the log scale), pathogens are recorded on about six times as many strawberry-like than fern species. There was a total of 141,050 citations to the 84 strawberry-like species (on average 1,679 per species) and 46 had at least one fungus record. There was a total of 197,744 citations to the 200 fern species (on average 99 per species) and 37 had at least one fungus record.

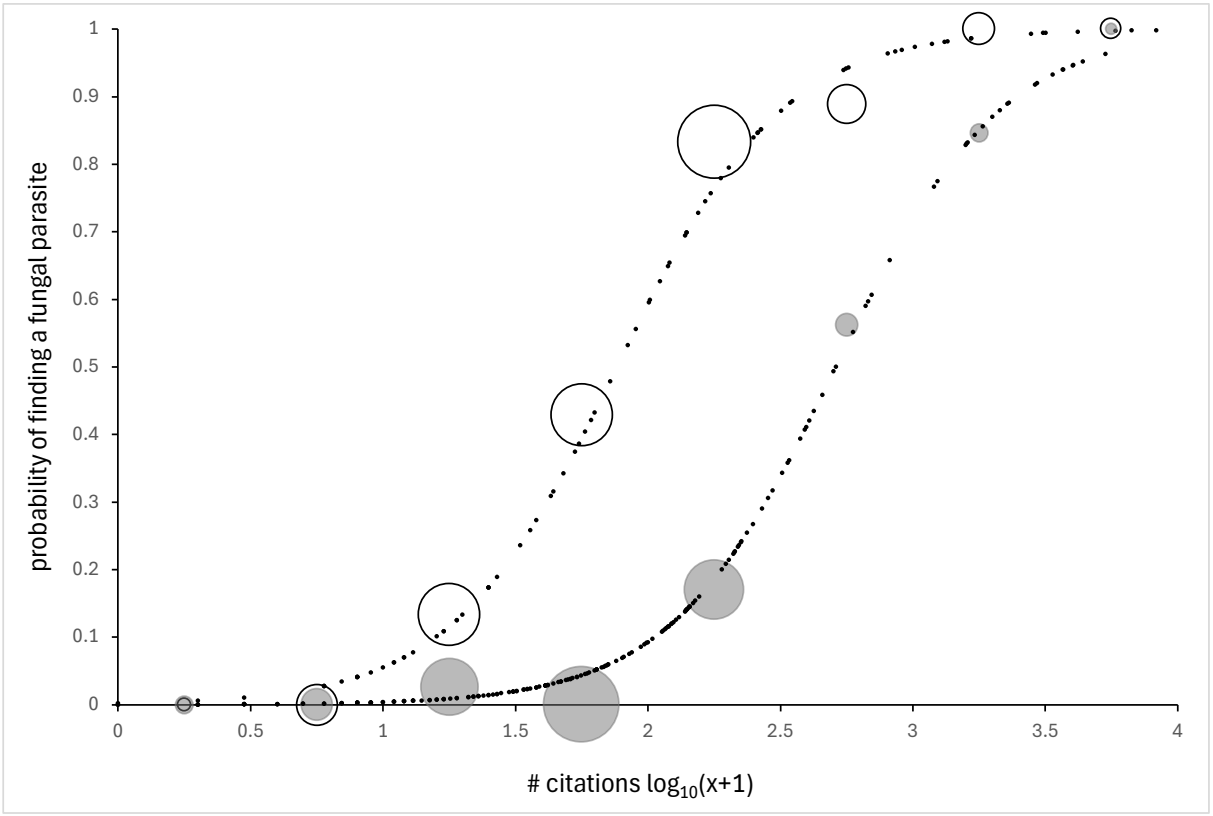

Figure 3: The relationship between probability of detecting a fungal parasite and number of citations to the host, back transformed from a linear logistic regression fit (see text). The points are values predicted from the logistic regression (upper series are strawberry-like plants). Open circles show observed probabilities for strawberry-like plants and closed circles show observed probabilities for ferns. Diameters of the dots are proportional to the number of citations in each of the classes.

Excluding host species with no fungal record rendered the interaction term of the glm (logFungi ~ logCitations * plantType) significant (***). The slope of the relationship between pathogen occurrence and number of citations was 0.59 (***) for strawberry-like plants (95% confidence interval: 0.501–0.684) and 0.29 (**) for ferns (95% confidence interval: 0.053 – 0.530). That is, the positive association between the number of citations and fungi recorded depended on the type of plant. If plants are strawberry-like (strawberries + cinquefoils), one unit of increase in log(citations) will, on average, give 0.59 units of increase in log(fungi). If plants are ferns, one unit increase in logCitations will, on average, give 0.29 units of increase in logFungi (fig. 4). Excluding the agronomically important strawberries from the strawberry-like plant type did not annul the significance of the interaction term (**). The above slopes (0.59 and 0.29) indicate that a ten-fold increase in the number of citations roughly quadrupled the records of fungi in strawberry-like plants, whereas it roughly doubled the one in ferns.

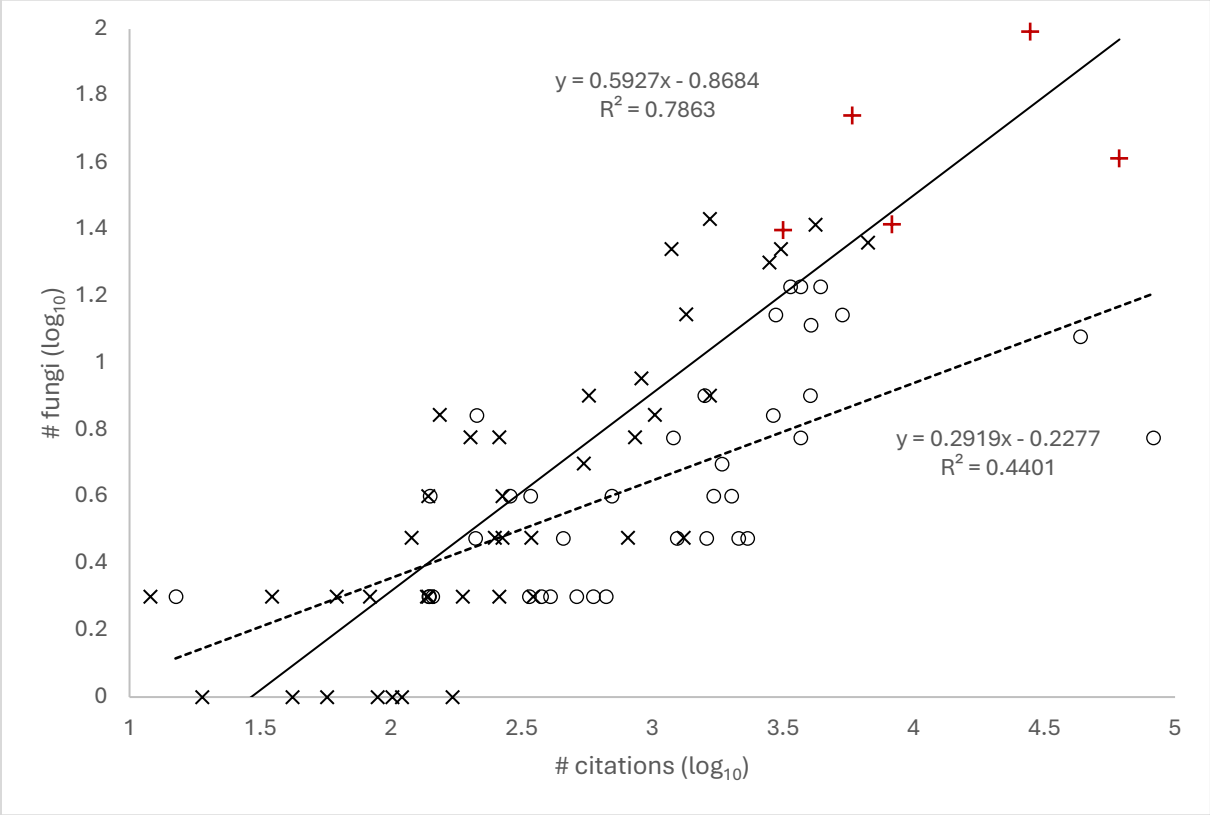

Figure 4: Fungal parasite richness of fern species and strawberry-like species in relation to study effort for each plant species. The estimate of the study effort for a plant species is its number of citations on a $\log_{10}$ scale. The estimate for the fungal parasite richness is the number of fungi recorded in the *USDA fungal databases* on a $\log_{10}$ scale. Open circles: fern species; crosses: strawberries and cinquefoils. Although they were treated as one sample, the markers differ for strawberries (red +) and cinquefoils (black ×).

2.3.1 Some details. Five of seven strawberry species are at the upper right of the distribution of all plant species. The two strawberry species for which no fungi have been recorded are *Fragaria bringhurstii* and *F. cascadensis*. *F. bringhurstii* is a wild (natural) hybrid of *F. vesca* and *F. chiloensis*. It has been discovered/described in 1999. Its range is limited to the Coast of California. None of its 5 citations retrieved by Scholar are about microbial parasites (tab. 1). *F. cascadensis* is a decaploid, wild strawberry that has recently been discovered/described (Hummer 2012; 2015). It is limited to a band high in the *Cascades* range of Oregon, USA. None of the 26 citations found by Scholar are about microbial parasites (tab. 1).

study category:	citations of: *F. bringhurstii*	*F. cascadensis*
discovery / description / biogeography	1	4
volatiles (aroma) / anthocyanins (colour)	-	4
ploidy / genetics / molecular / phylogeny	2	6
general reviews / evolutionary origins	2	2
germplasm conservation / breeding / gene-banks	-	4
multicellular animal pests of Fragaria	-	2
false retrieval / doublets / news items	-	3

Table 1: Topical categories of the articles citing the two Fragaria species with no fungal records in the USDA Fungal Databases.

Rumohra adiantiformis (G. Forst.) Ching, the leatherleaf fern, has 228 citations in Scholar and 38 records in the USDA Fungal Databases. The fern species in my random sample had a maximum of 16 fungi recorded (three species) and that at about 17 times the citations. This fern is of tropical origin and used as an ornamental plant. It is routinely propagated asexually, by dividing the rhizomes of the sporophytes, and this is known to increase its susceptibility to disease (Fonseka 2020, 113). Though anecdotal and speculative, this may be the reason why the number of fungi recorded for *R. adiantiformis* seems remarkably high among ferns.

Vittaria appalachiana Farrar & Mickel is an polyploid fern species that has no haploid or sporophyte stage (Farrar and Mickel 1991). It also happened to be no part of the above analysed random sample from ferns. Its so-called gametophytes produce no gametes but new gametophytes via strings of vegetative cells (gemmae). This differs from the asexual reproduction of other fern species, where the gametophytes vegetatively produce sporophytes. Here, the latter incur a cost (Mogie 1990; 1992, 43; 2013) of producing half as many unreduced spores as their sexual competitors could produce reduced spores (see section 2.1). The *USDA Fungal Databases* have no record for *V. appalachiana*. Searching Scholar for scientific studies of *V. appalachiana* that also report on its fungi (or pathogens, or plant diseases, etc.) neither yielded results. Whether this is a contingency or another paradox of pteridology cannot be guessed. If so, three paradoxes would be embedded in Matryoshka-style: 1. the general prevalence of sexual reproduction in animals and plants; 2. the high frequency of asexual reproduction combined with the low frequency of microbial parasites in ferns; 3. no parasitic fungi recorded for *V. appalachiana* despite its asexuality.

3. Discussion

Part 1

We revisited the pioneers of what has become known as the evolutionary paradox of sexual reproduction (part 1). Following narrowly some of their theoretical arguments lead to W. D. Hamilton's parasite red-queen model and George C. Williams' last challenge to it. Unfortunately, Hamilton had died unexpectedly, and Williams could only present it in a memorial talk (Trivers 2015, 195) and an obituary notice made from it (Williams 2000). This challenge has hitherto been ignored, except for a history-of-science article (Dagg 2017, 58). Williams raised the widespread life cycle of organisms like strawberries (diplontic and heterogonic, fig. 1), as a counterexample calling the red-queen model into question. Micro-parasites cannot maintain sexual reproduction in this huge group of organisms, Williams argued, because they propagate contrary to what would be adaptive under red-queen selection. Their recombinant offspring disperses, and their clonal offspring stays close to the parent. We took this to mean that the life cycle is a decisive context for the cost and maintenance of sexual reproduction. A life cycle seemed preferable for understanding, that spread out as far as possible the two costs of the sexual process, meiosis and male function (or fertilisation). We thus arrived at the diplohaplontic life cycle as the point of departure into a quantitative analysis, and at fern-like organisms as the best candidates for comparison with terrestrial, perennial, and herbaceous strawberry-like ones.

Part 2

The haploid spores of ferns are recombinant through meiosis and disperse before growing into haploid gametophytes. They produce haploid gametes that fuse to produce diploid zygotes. These are recombinant through syngamy. That is, recombination is spread out over the whole life cycle. The zygote grows into a sporophyte, in situ, on the maternal gametophyte. Staying offspring that is recombinant should do better under red-queen selection than the clonal offspring of strawberries. That ferns indeed have few microbial parasites turned out to be an aged lore among botanists (Berkeley 1862; Page 2002, 13). Helfer (2006) and Antonovics (2020) pioneered the quantitative analysis of fungal scarcity in ferns compared with forbs. Our new angle of approach suggests their life cycle as a potential explanation for this finding.

Combining the separate studies on fern infestation and the maintenance of sex, we tested strawberry-like plants (strawberries and cinquefoils) against ferns (see part 2). If Williams (2000) was right, these types of plants should not differ in their occurrence and number of fungi. Alternatively, fern-like species should have fewer fungi, because their life cycle is better adapted to red-queen selection by micro-parasites. Both the occurrence and number of fungi was significantly higher in the strawberry-like plants. This suggests that heterogonic life cycles with clonal staying offspring are not optimal vis-à-vis micro-parasites.

Overall conclusion

Heterogonic organisms of the strawberry model would be better off with recombinant staying offspring and clonal dispersing offspring. Yet, this would amount to sexually producing rhizomes, stolons, tubers etc. This may well-nigh be an evolutionary impossibility. Strawberry model organisms do not produce staying offspring asexually because that is optimal vis-à-vis microbial parasites, but because their life cycle did not offer a way to produce them sexually. In conclusion, strawberry model organisms do not exclude red-queen selection from their domain of life history, but this domain of life history is excluded from an optimal adaptation against micro-parasites. Ferns show that a life cycle exists that is better adapted to them. The pressure to maintain sexuality should be correspondingly higher in strawberry like organisms than in ferns. The finding that the frequency of asexuality is exceptionally high in ferns (Walker 1966, 155; Grusz 2016) agrees with this conclusion.

A surprising question remains: Why do heterogonic life cycles with dispersing clonal propagules and staying recombinant ones (henceforth referred to as *red-queen life cycles*) not dominate multicellular life? Micro-parasites were a selective force throughout the evolution of multicellularity. If dispersal meant escape from parental parasites, saving the cost of sex on dispersing propagules but incurring it for staying ones should be the best strategy against micro-parasites. A red-queen life cycle should be even better than the one of ferns spreading recombination (meiosis and syngamy) over the whole cycle. Yet, most multicellular species have different life cycles.

Searching for organisms with red-queen life cycles, a rare one seems to exists in haplontic Peritricha (Ciliophora) of the species *Zoothamnium alternans* and *Z. arbuscula* (Furssenko 1929; Summers 1938, 126; Herron et al. 2013, 11). A haploid colony produces haploid swarmers and microgamonts that disperse. The swarmer grows into a new haploid colony elsewhere, the microgamont disperses and fuses with a macrogamont of another colony. The resulting diploid part of that colony is recombinant through syngamy. It produces haploid

parts that are recombinant through meiosis. But these recombinant parts all stay part of their colony. That is, the recombinant offspring stays in situ, the clonal offspring (swarmer or microgamont) disperses. Most colonies produce only two macrogamonts that can fuse with microgamonts (Furssenko 1929; Summers 1938). This and the short lifespan of colonies limit the extent to which they can become genetic mosaics. [Colonies of the largest species of the genus, *Z. niveum*, live for seven days on average and up to 11 days (Ott, Bright, and Bulgheresi 2004; Rinke et al. 2007), though sexual reproduction has not been observed in this species, (Fauré-Frémiet 1930, 47; Rinke et al. 2007; Bright et al. 2014).]

Anyway, red-queen life cycles hardly form a considerable part of multicellular life.

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Appendix

1. List of ferns used in the study

CSV format: species, number of citations, number of fungi recorded; semicolons replace line breaks. Species names are not italicized, authority names are as in the USDA Plants Database.

Adenophorus montanus, 13, 0; Adiantum aleuticum, 336, 1; Adiantum capillus-veneris, 82403, 5; Adiantum fragile, 50, 0; Adiantum modestum, 22, 0; Adiantum pulverulentum, 147, 0; Adiantum tenerum, 43239, 11; Adiantum tracyi, 269, 0; Actinostachys inopinata, 11, 0; Actinostachys spirophylla, 1, 0; Anemia mexicana, 220, 0; Anemia portoricensis, 11, 0; Anopteris hexagona, 31, 0; Antrophyum plantagineum, 141, 0; Argyrochosma dealbata, 58, 0; Argyrochosma microphylla, 34, 0; Asplenium boydstoniae, 5, 0; Asplenium ebenoides, 295, 0; Asplenium flagrum, 2, 0; Asplenium kokeense, 5, 0; Asplenium morganii, 4, 0; Asplenium sphenocookii, 2, 0; Asplenium abscissum, 122, 0; Asplenium adiantum-nigrum, 1610, 2; Asplenium cookii, 20, 0; Asplenium hobdyi, 16, 0; Asplenium horridum, 57, 0; Asplenium macraei, 53, 0; Asplenium nidus, 3370, 16; Asplenium normale, 390, 0; Asplenium obtusifolium, 40, 0; Asplenium plenum, 40, 0; Asplenium polyodon, 375, 1; Asplenium pumilum, 150, 0; Asplenium trichomanes-ramosum, 155, 0; Asplenium tutwilerae, 8, 0; Asplenium varians, 113, 0; Astrolepis integerrima, 116, 0; Azolla microphylla, 2280, 0; Blechnum appendiculatum, 143, 0; Blechnum vulcanicum, 112, 0; Bolbitis aliena, 40, 0; Bolbitis pergamentacea, 21, 0; Botrychium acuminatum, 2, 0; Botrychium alaskense, 33, 0; Botrychium gallicomontanum, 30, 0; Botrychium matricariifolium, 423, 0; Botrychium mormo, 236, 0; Botrychium multifidum, 664, 1; Botrychium oneidense, 130, 0; Botrychium robustum, 37, 0; Botrychium simplex, 678, 0; Botrychium spathulatum, 45, 0; Botrychium tunux, 30, 0; Botrychium virginianum, 2310, 2; Campyloneurum angustifolium, 196, 0; Ceratopteris thalictroides, 2130, 2; Cheilanthes aemula, 41, 0; Cheilanthes fendleri, 142, 0; Cheilanthes lanosa, 502, 0; Cheilanthes lindheimeri, 137, 0; Cheiroglossa palmata, 79, 0; Coniogramme pilosa, 68, 0; Ctenitis nemorosa, 8, 0; Ctenitis sloanei, 84, 0; Ctenitis subglandulosa, 53, 0; Cyclopeltis presliana, 29, 0; Cyclopeltis semicordata, 140, 3; Cystopteris fragilis, 4390, 16; Cystopteris reevesiana, 63, 0; Davallia heterophylla, 70, 0; Davallia pusilla, 10, 0; Davallia trichomanoides, 211, 6; Dennstaedtia punctilobula, 2000, 3; Deparia marginalis, 26, 0; Deparia petersenii, 340, 3; Dicranopteris linearis, 4010, 7; Diellia lauii, 1, 0; Diellia mannii, 31, 0; Diplazium cristatum, 118, 0; Diplazium riedelianum, 15, 0; Diplazium sandwichianum, 119, 0; Diplazium striatum, 67, 0; Doodia lyonii, 16, 0; Doryopteris subdecipiens, 7, 0; Drynaria quercifolia, 1600, 0; Dryopteris mickelii, 7, 0; Dryopteris neowherryi, 15, 0; Dryopteris pittsfordensis, 14, 0; Dryopteris carthusiana, 2950, 13; Dryopteris cinnamomea, 51, 0; Dryopteris glabra, 98, 0; Dryopteris goldieana, 103, 0; Dryopteris intermedia, 1240, 2; Dryopteris ludoviciana, 224, 0; Dryopteris slossoniae, 21, 0; Dryopteris triploidea, 70, 0; Dryopteris tenebrosa, 3, 0; Elaphoglossum alatum, 35, 0; Elaphoglossum chartaceum, 14, 1; Elaphoglossum crassifolium, 63, 0; Elaphoglossum peltatum, 127, 0; Elaphoglossum petiolatum, 124, 0; Elaphoglossum spathulatum, 46, 0; Gaga kaulfussii, 50, 0; Grammitis aspleniifolia, 2, 0; Grammitis taxifolia, 17, 0; Gymnocarpium dryopteris, 2890, 6; Hemionitis palmata, 218, 0; Hymenophyllum asplenioides, 55, 0; Hymenophyllum decurrens, 12, 0; Hymenophyllum fragile, 30, 0; Hymenophyllum fucoides, 115, 0; Hymenophyllum lanceolatum, 24, 0; Hymenophyllum macrothecum, 7, 0; Hymenophyllum obtusum, 23, 0; Hypolepis hawaiiensis, 18, 0; Lastreopsis effusa, 69, 0; Lellingeria hartii, 8, 0; Lindsaea tetragona, 22, 0; Lindsaea walkerae, 24, 0; Lomagramma lomarioides, 11, 0; Marsilea macropoda, 99, 0; Marsilea mollis, 75, 0; Melpomense anfractuosa, 0, 0; Microlepia adulteriana, 0, 0; Microlepia speluncae, 512, 1; Nephrolepis acutifolia, 122, 0; Nephrolepis cordifolia, 1840, 4; Nephrolepis undulata, 212, 0; Niphidium crassifolium, 209, 2; Odontosoria scandens, 33, 0;

Oleandra articulata, 139, 1; Onoclea sensibilis, 5330, 13; Ophioglossum concinnum, 38, 0; Ophioglossum crotalophoroides, 248, 0; Ophioglossum pendulum, 395, 0; Ophioglossum polyphyllum, 201, 0; Ophioglossum reticulatum, 818, 0; Oreogrammitis palauensis, 3, 0; Osmunda cinnamomea, 4040, 12; Polypodium camptophyllarium, 12, 0; Pellaea brachyptera, 59, 0; Pellaea gastonyi, 37, 0; Pellaea glabella, 593, 1; Pellaea ovata, 139, 0; Phegopteris connectilis, 1200, 5; Pilularia americana, 321, 0; Platycerium superbum, 93, 0; Pleopeltis polylepis, 80, 0; Pleopeltis thyssanolepis, 34, 0; Polypodium californicum, 284, 3; Polypodium incognitum, 10, 0; Polypodium scouleri, 225, 0; Polypodium sibiricum, 63, 0; Polystichum calderonense, 8, 0; Polystichum kruckebergii, 62, 0; Polystichum kwakiutlii, 9, 0; Polystichum munitum, 3690, 16; Polystichum tsussimense, 20, 0; Pteridium arachnoideum, 698, 3; Pteris ensiformis, 1580, 7; Pteris excelsa, 143, 1; Pteris lydgatei, 4, 0; Pteris pungens, 48, 0; Stenochlaena palustris, 1710, 3; Sticherus brevipubis, 8, 0; Tectaria amesiana, 10, 0; Tectaria estremeriana, 0, 0; Thelypteris augescens, 49, 0; Thelypteris balbisii, 46, 0; Thelypteris cordata, 9, 0; Thelypteris palmeri, 1, 0; Thelypteris rolandii, 7, 0; Thelypteris exindusiata, 2, 0; Thelypteris germaniana, 12, 0; Thelypteris hastata, 6, 0; Thelypteris hispidula, 138, 1; Thelypteris ovata, 86, 0; Thelypteris palauensis, 3, 0; Thelypteris palustris, 3680, 5; Thelypteris quelpaertensis, 40, 0; Thelypteris resinifera, 27, 0; Thelypteris sancta, 16, 0; Thelypteris wailele, 6, 0; Tomophyllum inconspicuum, 1, 0; Trichomanes angustifrons, 26, 0; Trichomanes hymenoides, 25, 0; Trichomanes kapplerianum, 18, 0; Trichomanes membranaceum, 41, 0; Trichomanes minutum, 43, 0; Trichomanes polypodioides, 96, 0; Trichomanes rigidum, 118, 0; Trichomanes robustum, 22, 0; Trichomanes scandens, 66, 0; Vittaria graminifolia, 189, 0; Woodsia glabella, 454, 2; Woodsia gracilis, 6, 0; Woodsia oregana, 406, 1.

2. List of strawberry-like plants (strawberries & cinquefoils) used in the study

CSV format: species, number of citations, number of fungi recorded; semicolons replace line breaks. Species names are not italicized, authority names are as in the USDA Plants Database.

Duchesnea indica, 3170, 25; Fragaria ananassa, 61300, 41; Fragaria bringhurstii, 5, 0; Fragaria cascadensis, 26, 0; Fragaria chiloensis, 5820, 55; Fragaria vesca, 28000, 98; Fragaria virginiana, 8290, 26; Potentilla acuminata, 5, 0; Potentilla alba, 804, 3; Potentilla albiflora, 11, 0; Potentilla ambigens, 60, 0; Potentilla angelliae, 7, 0; Potentilla anglica, 260, 6; Potentilla argentea, 2800, 20; Potentilla arguta, 1020, 7; Potentilla atrosanguinea, 559, 0; Potentilla basaltica, 18, 0; Potentilla biennis, 89, 1; Potentilla biflora, 137, 2; Potentilla bimundorum, 11, 0; Potentilla bipinnatifida, 57, 1; Potentilla brevifolia, 24, 0; Potentilla buccoana, 9, 0; Potentilla canadensis, 1180, 22; Potentilla cinerea, 172, 1; Potentilla collina, 120, 3; Potentilla concinna, 188, 2; Potentilla cottamii, 16, 0; Potentilla crinita, 54, 0; Potentilla cristae, 10, 0; Potentilla diversifolia, 547, 5; Potentilla drummondii, 83, 2; Potentilla effusa, 52, 0; Potentilla elegans, 43, 0; Potentilla erecta, 6690, 23; Potentilla fissa, 110, 1; Potentilla flabellifolia, 154, 7; Potentilla fragiformis, 47, 0; Potentilla furcata, 7, 0; Potentilla glandulosa, 908, 9; Potentilla gracilis, 1350, 14; Potentilla grayi, 5, 0; Potentilla hickmanii, 37, 0; Potentilla hippiana, 350, 2; Potentilla hookeriana, 101, 1; Potentilla inclinata, 267, 4; Potentilla intermedia, 201, 6; Potentilla macounii, 6, 0; Potentilla matsuokana, 7, 0; Potentilla millefolia, 12, 2; Potentilla morefieldii, 16, 0; Potentilla multijuga, 24, 0; Potentilla multisecta, 15, 0; Potentilla nana, 24, 0; Potentilla neumanniana, 259, 2; Potentilla newberryi, 35, 2; Potentilla nivea, 857, 6; Potentilla norvegica, 1660, 27; Potentilla oblanceolata, 0, 0; Potentilla ovina, 118, 0; Potentilla paradoxa, 250, 3; Potentilla pectinisecta, 19, 1; Potentilla pensylvanica, 344, 3; Potentilla plattensis, 71, 0; Potentilla pseudosericea, 18, 0; Potentilla pulchella, 139, 4; Potentilla pulcherrima, 267, 3; Potentilla recta, 3100, 22; Potentilla reptans, 4200, 26; Potentilla rimicola, 8, 0; Potentilla rivalis, 139, 2; Potentilla robbinsiana, 164, 0; Potentilla rubella, 7, 0; Potentilla rubida, 2, 0; Potentilla rubricaulis, 100, 0; Potentilla rupestris, 317, 9; Potentilla rupincola, 32, 0; Potentilla sierrae-blancae, 10, 0; Potentilla simplex, 1660, 8;

Potentilla sterilis, 571, 8; Potentilla stipularis, 62, 2; Potentilla subjuga, 42, 1; Potentilla tundricola, 1, 0; Dasiphora fruticosa, 1320, 3.