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What does the geography of parthenogenesis teach us about sex?

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Theory predicts that sexual reproduction is difficult to maintain if asexuality is an option, yet sex is very common. To understand why, it is important to pay attention to repeatably occurring conditions that favour transitions to, or persistence of, asexuality. Geographic parthenogenesis is a term that has been applied to describe a large variety of patterns where sexual and related asexual forms differ in their geographic distribution. Often asexuality is stated to occur in a habitat that is, in some sense, marginal, but the interpretation differs across studies: parthenogens might not only predominate near the margin of the sexuals' distribution, but might also extend far beyond the sexual range; they may be disproportionately found in newly colonizable areas (e.g. areas previously glaciated), or in habitats where abiotic selection pressures are relatively stronger than biotic ones (e.g. cold, dry). Here, we review the various patterns proposed in the literature, the hypotheses put forward to explain them, and the assumptions they rely on. Surprisingly, few mathematical models consider geographic parthenogenesis as their focal question, but all models for the evolution of sex could be evaluated in this framework if the (often ecological) causal factors vary predictably with geography. We also recommend broadening the taxa studied beyond the traditional favourites.

This article is part of the themed issue 'Weird sex: the underappreciated diversity of sexual reproduction'.

1. Introduction

The term 'parthénogenèse géographique' was coined in 1928 by Albert Vandel, a French zoologist and early biospeleologist (i.e. a researcher of cave-dwelling organisms) [1]. His work replaced the earlier concept of 'geographic spanandry'—a term used to describe that males of some species became rarer with higher latitudes. In the arthropods he studied, Vandel noted that spanandry was owing to the increasing prevalence of obligate parthenogenetic forms of the same morphospecies, making the phrase 'geographic parthenogenesis' a more precise explanation for the rarity of males. He recognized that the latitudinal pattern, which he found in some species but not others, was but an instance of geographic parthenogenesis in general, that he defined as a phenomenon where a sexual and a parthenogenetic form of the same species occupy distinct geographic areas, though with potential overlap [1]. Modern definitions concern more broadly asexual organisms that have different distributions from their closest living sexual relatives (a pragmatic solution to the problem that species concepts enter a zone of ambiguity once some lineages are asexual).

Since then, other trends have been proposed for the distribution of asexuals compared with their sexual counterparts, and all appeared for the first time in 1978 in a paper by Glesener & Tilman [2]. Modern introductions to the phenomenon of geographic parthenogenesis often focus on a co-occurrence of three patterns [3,4]: first, parthenogens tend to have a wider distribution than their sexual counterparts [3]; second, they tend to occupy higher latitudes (mostly studied in the Northern Hemisphere [5]; but see [6,7]) and third, they tend to occur in higher altitudes [8]. In addition to the above-mentioned broad patterns, a disproportionate occurrence of parthenogens in arid habitats compared with their sexual counterparts (e.g. [6,9] in Australian lizards), on islands or island-like habitats [10] or 'disturbed' habitats [11], which may or may not be associated with humans (see [12]), has been proposed.

Intriguingly, one of the early patterns proposed by Glesener & Tilman [2], namely that parthenogens disproportionately occupy continental rather than maritime regions, has disappeared from the literature. Their statement concerning a trend to drier habitats appears to be based on one single example, *Trichoniscus elisabethae*, cited in [1,13], where a parthenogen was found both in the coldest and driest edges of the sexual distribution. To this day, it is difficult to judge to what extent aridity is a general trend among parthenogens (see §3a).

Some sexual and asexual pairs do not follow any of the trends listed above [14,15], or even show an opposite pattern [16]. It is difficult to estimate what fraction of geographic parthenogenesis cases they represent, as exceptions may receive less attention than cases that confirm the expectations and end up being ignored in synthetic works and reviews on the topic [8,17]. While some authors implicitly use 'geographic parthenogenesis' to specifically refer to the occurrence of patterns in the expected (directional) direction, we here stick to the broad definition given by Vandel that includes any kind of geographic difference in reproductive mode.

(a) A marginal habitat?

Overall, the geographic margins of a species distribution, potentially occupied by parthenogens, are often equated with ecological marginality, and various authors expand differently on the term. Descriptions include low-stability, transient or disclimax habitats [10,18–20], metapopulation structure with colonization–extinction cycles [21,22], low amount or diversity of resources [2,23], low population productivity [24], low density [25,26], high openness and habitat vacancy [20,27] and higher abiotic than biotic selection pressure [2].

The diversity of characterizations above highlights a problem: it is difficult to pinpoint the precise meaning of 'marginal' habitats, given that most reports of geographic parthenogenesis are purely descriptions of sexuals and asexuals' range. It should be obvious that numerous biotic and abiotic factors will vary along the way from the 'core' to the 'margin', which gives a researcher perhaps too much freedom to focus on any one dimension of variation. Explaining species distribution, in general, has been a long-standing question in ecology, but field evidence of the factors limiting any species boundaries are still surprisingly scarce, lagging well behind theory [28]. In the case of geographic parthenogens, it is difficult to judge which definition of 'marginality' is likely to suit most systems. Only in recent years have studies begun to characterize the actual niche differences between sexuals and asexuals in some model species. For instance, Schmit *et al.* [29] suggested that sexual *Eucypris virens* persisted only in ponds with a sufficiently unpredictable hydroperiod, whereas asexuals dominated more stable ponds; and Verduijn *et al.* [30] identified microecological preferences of sexual and asexual dandelions that might explain their large-scale distribution, considered a typical instance of geographic parthenogenesis.

Finally, the notion of marginality, either geographic or ecological, is difficult to defend in species where asexuals occupy a much wider geographic area than sexuals (e.g. buttercup *Ranunculus auricomus* [3], weevil *Otiorhynchus scaber* [31]). Larger ranges seem instead more consistent with the second feature of many areas occupied by parthenogens: they have been more recently opened to colonization. This argument extends over variable time scales, from habitats recently created by humans (e.g. ponds [32] or forest tracks [33]), to islands [10] and, most notably, to zones that became progressively available after the last ice age [8,13]. Note that longitudinal differences in distribution are not considered a typical pattern of geographic parthenogenesis, but as emphasized by Bell [18], they can nonetheless reflect the direction the climate envelope moved, opening new habitats in its wake. Distance from the closest glacial refugia might in this respect be the relevant metric, with differences in latitude being only one of its most obvious correlates.

This debate points at interesting differences between explanations that all, at first, appear superficially to be simply different manifestations of the term 'marginal'. There are aspects of the pattern that encourage researchers to seek ecological explanations inherent to current habitat, whereas others emphasize the importance of temporal aspects of the evolutionary history.

(b) To what extent do the parthenogens share common features?

Leaving aside the definitional minefield of prokaryotic sex or asex (see [34–36]), examples of parthenogenesis can be found in all major groups of eukaryotes. Given that parthenogenesis is a derived trait (sex in eukaryotes being ancestral), it is unsurprising that it does not manifest itself in the same way in all instances. Broadly, parthenogenesis is defined as a form of asexual reproduction where the zygote derives from an unfertilized female gamete [37]. It thus contrasts with selfing, where fertilization occurs between gametes produced by the same individual (e.g. in plants [38], animals, [39], fungi [40]), and with vegetative reproduction, where the new individual stems from a collection of somatic cells which usually results in relatively lower dispersal compared with the production of zygotes (e.g. plants [41], animals [42], fungi [43], algae [44]).

The founder of the term geographic parthenogenesis himself remarked that a northerly distribution of asexuality was probably not restrained to parthenogenetic species: Vandel cites instances of aquatic angiosperms that reproduce solely via bulbils in the north of Europe [1]. However, vegetative reproduction is often ignored in discussions concerning the evolution of sex; thus the parallel drawn by Vandel has been left largely unexplored. Yet, selfing, vegetative reproduction and parthenogenesis share some common traits, and conversely, there is much diversity among parthenogens themselves. One instance is that the well-known demographic cost of male production (the twofold cost of sex) does not apply to hermaphrodites, for which the cost of sex results from a different process [45].

The origins of parthenogenesis are not always known. Some cases have been linked to the action of bacterial endosymbionts (many arthropods [46]); parthenogenesis-inducing mutations have been identified in a few cases (e.g. in *Daphnia* [47], aphids [48], some angiosperms [49]), and large-scale genomic events are often suspected to have either directly or indirectly caused the evolution of parthenogenesis [10]. In many lineages, parthenogenesis is indeed associated with past hybridization, often along an increase in ploidy [1,10]. A few autopolyploid lineages (i.e. polyploids resulting from genome duplication) are also found to be parthenogenetic. Note that polyploidy is also a frequent feature of selfing plants [50].

Those correlates can have different implications for the fitness of parthenogens (see §2). Moreover, the developmental routes that have evolved to circumvent standard meiosis are also diverse, and this can lead to differences in key genetic and ecological properties of parthenogens [51], as we shall discuss now.

Reproduction with no need for a partner is a feature of vegetative reproduction, self-fertilization and many forms of parthenogenesis, but not all: cases exist where zygote development requires sperm or pollen as a trigger of embryogenesis, but the offspring still develops parthenogenetically as the sperm or pollen makes no genetic contribution. This quirky system is known as gynogenesis in animals [52] and pseudogamy in plants (most parthenogenetic angiosperms [53]).

Clearly, geographic distributions of the parasitic asexual form cannot expand past their sexual hosts, when parthenogens strictly rely on a male function as a developmental trigger. Still, some pseudogamous species are very widespread, thanks to one of two tricks. First, the absence of karyogamy can make the spectrum of suitable host species wider, allowing the parthenogens to expand outside, and exceed, their original sexual parents' range (e.g. earthworm *Lumbricillus lineatus*, fish *Poecilia formosa* [19]; see also [54] for an invasive hermaphroditic clam that uses androgenesis: sperm 'hijacks' eggs produced by other hermaphrodites which then develop as clones of their father, as the maternal genome is eliminated). Second, hermaphrodites can combine the production of parthenogenetic eggs and sperm, which then can be used to trigger parthenogenetic reproduction in either other conspecifics (e.g. sperm-trading planarians [42]) or themselves (self-compatibility commonly evolves in pseudogamous plants [53]). Interestingly, the former category frees the parthenogens from the constraint of having to coexist with the parental sexual species, which can be ecologically a very difficult form of coexistence [55]. Instead, reproduction is now dependent on the presence of conspecific parthenogens: it is therefore a rare case of parthenogenesis without the capacity for fully uniparental reproduction. The latter category is demographically extremely similar to self-fertilization (selfing), though with potential genetic differences.

Selfing is an extreme form of inbreeding, which eventually leads to complete homozygosity. Some forms of parthenogenesis similarly involve the ploidy-restoring fusion of two products of meiosis, and if the fusion occurs late in the process of oogenesis (terminal fusion automixis [56]), the genetic consequences of parthenogenesis and selfing are identical. Total homozygosity, on the other hand, can instantly occur in lineages using gamete duplication to restore ploidy [51]. Some other types of asexuality will typically 'freeze' the levels of heterozygosity in a clonal lineage. This happens in vegetative reproduction, as the propagule contains somatic cells, and also in some forms of parthenogenesis. Two types of parthenogenesis can achieve this: in central fusion automixis, the two products of the reductional division of meiosis fuse to restore ploidy, whereas in apomictic parthenogenesis, meiosis is totally suppressed, which makes parthenogenesis functionally mitotic (note that this statement uses a definition different from the broad botanical use of the term 'apomixis' where it refers to all forms of asexual production of seeds [57]). Apomictic parthenogenesis is the most frequent type of parthenogenesis [51]. In forms of parthenogenesis that, instead, use fusion of meiotic products, recombination can still occur. As this results in erosion of heterozygosity, some lineages are thought to have evolved to suppress recombination for this reason [58], yet this might also provide ways of purging deleterious mutations [59].

On top of intra-individual genetic diversity, population-level diversity also varies widely in parthenogens: it can go all the way from a unique clonal genome [60] to a diversity higher than sexuals (e.g. [61] in Collembola). Intriguingly, some species comprise single clones over very large areas (e.g. millipede *Nemasoma varicorne* in Denmark [62]), whereas in others, each clonal genotype occupies a very narrow range (e.g. *Ranunculus auricomus* [63]). This diversity can be ancient and stem from several independent origins. Alternatively, the generation of new asexual genotypes can still be ongoing, for instance via mutation [64], continuing hybridization of, or with, the sexual parents [65], contagious asexuality via endosymbiont transmission [66] or rare crossings with sexuals (e.g. [42] in hermaphrodite flatworms; [67] in *Daphnia* and [68] in *Artemia* owing to rare parthenogenetic sons), or forms of 'parasex' [69] such as horizontal gene transfer between individuals (bdelloid rotifers, see [70]) or introgression of environmental DNA (anhydrobiotic rotifers or tardigrades [71]).

If, as seems to be the case, asexuality comes in different 'flavours'—species can be found that are various combinations of polyploid, hybrid, host of manipulative symbiont, autonomous or sperm-dependent, relatively homo- or heterozygous, with low or high genetic diversity—then it may be hard to predict clear rules for geographic parthenogenesis that could be repeatably observed across taxa. It is therefore no wonder that it has been difficult to find a unifying explanation for the phenomenon.

2. Explanations for the main patterns of geographic parthenogenesis

We now turn our attention to published arguments (both verbal and mathematical) to explain the geographic distribution of parthenogens in higher altitudes, latitudes, islands, disturbed environments or over a larger area than their sexual relatives. Table 1 lists mathematical models that either directly address the phenomenon or that include a conclusions section where the authors discuss the model's implications for geographic parthenogenesis. Given the diversity we have discussed in the preceding section, it is clear that none of the formal or verbal models apply to all types of parthenogens, or to all potential patterns that have been discussed in the literature. One can nevertheless identify what the ultimate goals should be, aside from scenarios where sexuals might not reach certain areas in the first place, whereas asexuals, once they have emerged, can. Any model should explain (i) why sexuals are not outcompeted to extinction owing to the various costs associated with sex and (ii) conversely, once it predicts that sexuals can persist, why they do not do so throughout the entire range. In other words, it should address the two sides of the coin: why sex (here) and why asex (there)? Intriguingly, the default state, and hence the question asked, subtly differs between models. Some assume a baseline demographic cost to sex (table 1, 'democost' > 1), and by proposing a counteracting advantage, they look for conditions where this advantage is realized sufficiently to favour sex. On the other

Table 1. Mathematical models of geographic parthenogenesis differ in their assumptions about parthenogens and in their ecological outcomes. YES, explicit focus of the model; Y, model implicitly applies to it; ~, model would need modifications to include this assumption; N, model structure conflicts with this assumption. First three columns concern the assumptions made regarding parthenogens' degree of uniparentality (autonomous/pseudogamous/pseudogamous hermaphrodite), the next two columns indicate assumptions regarding homozygosity (apomictic/automictic). The 'sexes' column indicates whether the model assumes a gonochorous species (♀ + ♂) or an outcrossing hermaphrodite (⚥ (out)). The 'democost' column indicates the reproductive output of asexuals compared with sexuals in the model; 2 means that total fecundity is the same but: in a gonochoristic context the number of female offspring is doubled; in a hermaphroditic context male function resources are reallocated to female function. Models also differ in their assumptions about spatial structure, mating among sexuals (or possibility for crosses between asexual male function and sexual females), dispersal and clonal diversity, as indicated. The final columns include whether clonal diversity is a requirement of the mechanism leading to a geographic parthenogenesis pattern (column 'diversity required?'), what this mechanism is, where the asexuals are predicted to prevail, whether coexistence of sexuals and asexuals is possible, and the temporal pattern predicted.

paper	auto-nom.	pseudog.	pseudog.+ hermaphro.	apo-mictic	auto-mictic	sexes	democost	space	mating	dispersal	clonal diversity	diversity required?	mechanism leading to geographic parthenogenesis	habitat of asexuals?	coexistence?	stable?
Variability and competition for resources																
Gaggiotti [23]	YES	Y	Y	Y	Y	⚥ (out)	[1 ; 2]	patches with heterogeneous competition	random (space, genotype)	random	implicit, lower than sexuals	N	competitive asymmetries	lower competition/more structured resource/lower diversity of sexuals	partial asexual refugium	stable
Weeks [72]	YES	Y	Y	Y	Y	⚥ (out)	2	1 patch, stable or fluctuating resource	random (no space)	n.a.	explicit (ongoing lineage generation)	Y	fluctuating environment favours phenotypic diversity	more stable resource	dynamic equilibrium	
Scheu *et al*. [73]	YES	Y	Y	Y	Y	♀+♂	2	one patch, regrowing resources	random (no space)	n.a.	explicit (ongoing lineage generation)	Y	competitive asymmetries	lower competition = higher mortality /more stable resource/regrows faster/larger population	N	stable
Song *et al*. [74]	YES	Y	Y	Y	Y	♀+♂	2	continuous, latitudinal gradient in resource / death rate	local, random	short-distance, random (migration rate affects coexistence)	explicit (ongoing lineage generation)	N	competitive asymmetries	lower competition = higher mortality /more stable resource/regrows faster/larger population	Y (for intermediate migration rate)	stable
Barrier against outbreeding																
Peck *et al*. [24]	YES	Y	Y	Y	~	⚥ (out)	[0.7 ; 1]	discrete, South–North gradient of productivity	local, random	random	low (ongoing lineage generation and selection)	Y/N	outbreeding depression of sexuals	sink habitat	Y (gradient)	stable
Mutation accumulation in space																
Salathé *et al*. [75]	YES	N	Y	Y	~	⚥ (out)	2	homogeneous grid	local, random	short-distance, random	deleterious mutation accumulation	N	mutational meltdown prevents invasion of large pop	small pop	N	stable
Contagious asexuality																
Britton & Mogie [76]	YES	N	~	Y	N	⚥ (out)	<1	continuous, homogeneous	local, random; asexual ♂ ×sexual ♀	local (diffusion)	n.a.	N	contagious asexuality	newly opened (verbal extrapolation)	yes (long-term)	slow asexual spread

hand, some models take the overall superiority of sex for granted ('democost' < 1), and seek special properties of asexuality that confer it an advantage in some contexts, making the question of geographic parthenogenesis more about 'why asex?' than 'why sex?'

(a) Neutral models regarding asexuality

In order to assess the explanatory power of adaptive hypotheses concerning the distribution of parthenogenesis, it is important to first consider expectations under a neutral model that does not resort to benefits or costs of asexuality *per se*, but to spatially varying probabilities of appearance [3,13] or persistence [8,19] of new asexual lineages.

The environments where asexual lineages originate could offer elements of explanation for their current distribution, if the probability of transition from sexuality to asexuality varies spatially. Hörandl [3] describes a scenario of 'opportunistic geographic parthenogenesis': climate change can make species ranges split, contract or expand, which then can create opportunities for hybridization, which in turn are known to have played a role in the origins of many parthenogenetic species (e.g. direct experimental evidence [77]; genetic inference [27]). Moreover, cold spells, variable temperatures and water stress can sometimes trigger the production of unreduced gametes [78]. If climate impacts the transition rate to asexuality, then 'hotspots' for parthenogens can be predicted to be in areas with fast-paced climate change in the recent evolutionary past. Elevated occurrence of asexual forms in previously glaciated areas, in particular, has been argued to support this idea.

Emergence must be followed by persistence for geographic parthenogenesis to be observable. A newly arisen parthenogenetic lineage is surrounded by sexuals, and as a rare cytotype, is endangered by destabilizing hybridization with the parental sexuals [19,79]. Persistence through this critical phase should be easier if an asexual lineage can exist in an area free of sexuals. Climate change provides newly opened environments, by driving the retreat of glaciers or deserts, or simply by shifting a species' suitable climatic envelope over new territories. Only those asexuals that happened to colonize them (by chance, as under the neutral model they are not better colonizers *per se*) remain observable today. Boundaries could then get stabilized by evolution of reproductive barriers, or a lethal hybrid zone equally detrimental to sexuals as asexuals [8,19,79].

Geographic differences arise in this 'neutral' model, because asexuals are simply assumed to persist better when they are not coexisting with sexuals, and the two types do not reach all areas. This hypothesis does not require differences in dispersal capacity between reproductive modes, but a limited capacity of both: in the absence of differences in competitive ability, the establishment patterns are expected to maintain significant geographic structure only if areas are not continually bombarded by sustained invasion efforts of each type. This hypothesis also relies on the fact that transitions from sexuality to asexuality are much more frequent than the reverse.

(b) Models in which correlates of parthenogenesis rather than parthenogenesis itself matter

There is also a class of models that, unlike the null models, accept that asexuals and sexuals can differ, but retain the view of the null models that asexuality *per se* might not be the driver behind patterns of geographic parthenogenesis. Instead, these models focus on traits that covary with asexual reproduction: polyploidy and hybridity [80]. The former was already present in the writings of Vandel [1] and Suomalainen [13], whereas the latter remained little discussed until Kearney *et al*. [8]. While hybridization between two species or genetically distant populations is usually deleterious [81], hybrids sometimes enjoy hybrid vigour and are fitter than either parent [82,83]. If associated with parthenogenesis (itself possibly a direct outcome of hybridization [77]), the fitness advantage will be conserved. Similarly, polyploidy is argued to confer a set of advantages such as larger cells, more gene expression, less sensibility to deleterious mutations and more evolutionary potential thanks to gene redundancy [84], which might provide an advantage in colonizing harsher environments [85], although this argument should not be taken at face value. For instance, in a species of Japanese ferns, sexuals are found at higher latitudes, altitudes and colder places than parthenogens, as the latter's larger, polyploid cells are more sensitive to freezing owing to their high water content [16].

Because most asexual species featured in the geographic parthenogenesis literature are both hybrid and polyploid, disentangling these effects is tricky. This triggered a debate that appears to have ended without a resolution, in the absence of any clearer way to cut than a few available counter-examples in both camps [8,86,87]. Of course, there is no reason why the two hypotheses should be mutually exclusive (while it remains a valid question which of these might be the stronger driving force).

It is clearly instructive to look at parallel questions asked in purely sexual lineages, as hybridity and ploidy changes can both occur without a transition to asexuality. Here, studies focusing on range size have given mixed results. The effect of diploid hybridity seems unpredictable (reviewed in [88]). Autopolyploidy (i.e. genome duplication) has been stated to lead to larger ranges than diploid parents in plants ([89], but see [26] for an opposite view), but we know of no formal meta-analysis of the question. Allopolyploidy, i.e. hybrid polyploidy, does not seem to correlate to larger ranges either [90], but intriguingly, two extensive studies in plants show it is more frequent in high latitudes [91] and in invasive plant species [92]. The abundance of polyploid morphs in northern biota, termed 'geographic polyploidy', was already an object of speculation by Vandel [1].

Of course, parthenogenetic reproduction may interact with the above advantages. If asexuality helps stabilize a hybrid or polyploid genome against meiotic disturbances or deleterious introgression, then it could allow a species to make the most of the advantages of either [26]. As a whole, one could imagine fruitful ways to bring some new light into the debate by focusing on taxonomical groups where parthenogenesis occurs without hybridity or polyploidy, for instance, in certain haplodiploid insects and mites made parthenogenetic by an endosymbiont [72,93], or diploid scale insects [94]. These are largely absent from the geographic parthenogenesis literature to date.

(c) Uniparentality and its effect on colonizing abilities

We now turn our attention to ideas involving demographic effects of parthenogenesis. Uniparentality is an obvious potential explanation for the increase in frequency of parthenogens further away from the glacial refugia, in disturbed areas, islands and marginal ecological niches. All else being equal, the ability to establish a population from a single individual predicts improved colonizing abilities, and there are two components to asexuality that can help: reproductive assurance, which is the ability to reproduce without finding a mate, and demographic advantage, incurred if parthenogens avoid paying the twofold cost of sex. This is an extreme form of the general demographic principle that female-biased populations can invade faster [95,96]. Note that dispersal ability *per se*, i.e. the ability to cover (and survive) a certain distance, need not differ. To the best of our knowledge, no difference in dispersal abilities between asexual and sexual propagules has been reported, apart from the obvious differences between short-distance vegetative (asexual) spread and the longer-distance spreading of (sexual or asexual) seeds. Potential differences should be investigated more closely, as dispersal in time and space can provide an alternative to sex in dealing with parasites and environmental uncertainty [97].

Reproductive assurance is only advantageous in cases where sexuals suffer from a low density of potential mates (mating Allee effect [98]): for instance, in newly open, resource-poor or high mortality habitats, areas with a low availability of pollinators or a short growing season (e.g. [99] in mixed populations of sexual and asexual *Drosophila*). The disproportionate presence of asexual plants in newly deglaciated areas compared with their sexual parents [90], suggests that the wave of recolonization from glacial refugia was largely dominated by asexuals [3]. The temporal dynamics are obviously of interest here. This is a challenging research question as it is far easier to gain access to 'snapshot' data than long time series. Even so, cases have been documented where sexuals are catching up on asexuals ([10] in cricket *Saga pedo*; [100] in grass *Poa fendleriana*), lending support to the idea that asexuals were simply faster in colonizing. Theoretically, the opposite can happen with contagious asexuality, which can make the distribution of sexual populations shrink over time (e.g. [67] in *Daphnia pulex*; [76]).

As in §2b, it is useful to draw parallels with fully sexual systems. In selfing plants, 'Baker's law' [101,102] was formulated to refer to the enrichment of self-compatible species in island ecosystems. A review of the geographic distribution of self-pollinating plants [38] shows that selfing species consistently have larger ranges than their strictly outcrossing relatives. In a review of the true implications of this law, Pannell *et al*. [103] show that uniparentality is expected to be advantageous in four contexts, similar to those discussed in geographic parthenogenesis: colonization of remote places by long-distance dispersal (island-like habitats), range expansion, colonization by invasive species and repeated colonization in metapopulations with frequent extinctions.

(d) Early selection on clonal lineages: frozen niches and general-purpose genotypes

In order to observe successful parthenogens, not every transition to asexuality has to succeed; it is sufficient that some do. As pointed out by Lynch [19], as selection acts on some newly emerged asexual lineages, the survivors will be the ones fortuitously blessed with favourable combinations of traits (clonal selection). Compared with those highly fit asexuals, sexuals incur a genetic cost of sex, as it breaks beneficial allelic combinations. This has led to two hypotheses to explain the ecological success of parthenogenesis provided many independent transitions within a lineage: the frozen niche variation, and the general-purpose genotype. Empirical support for both hypotheses is synthesized in [11].

First, the frozen niche variation hypothesis [104] states that a diverse array of clones, all representing a different microspecies, can together occupy more niches than sexuals, as sex always pulls the phenotypic distribution of the latter back towards the mean [105]. Note that the name should not be taken to imply that the population dynamics are in any way 'frozen', e.g. in snails *Potamopyrgus antipodarum*, a diverse array of clones has been shown to resist to co-evolving parasites via successive frequency-dependent selection of different genotypes [106].

Second, the general-purpose genotype hypothesis [25,107] states that clonal selection in a fluctuating environment would favour a clone that freezes a polyvalent genotype, which allows it to survive many conditions (a possibility enhanced by hybridization [19,25]). If the asexual population consists of such generalists only, then they are expected to be outcompeted by specialized sexuals (or specialized clones) wherever local conditions are stable enough (and dispersal is limited enough) for local adaptation to be important. However, in highly variable habitats at the margins of their competitors, general-purpose genotypes would thrive while specialists go extinct (bet-hedging, see [108]). This echoes the vision of parthenogens as fugitive or 'weed' species [25,109].

(e) Ecological conditions impact the relative benefits of sex

In this section, we review hypotheses that focus on how the benefits of sex might vary with ecology. Each hypothesis takes for granted a demographic advantage of asexuality (no cost of male production), and highlights how counteracting benefits of sex can vary spatially, tipping the balance in favour of one or the other reproductive mode.

One of the strongest candidate theories so far to explain how sex persists despite its demographic costs is that of the Red Queen [110]. The permanent need to escape biotic (and hence evolving) challenges, such as parasitism or interspecific competition, drives an evolutionary arms race, in which non-recombining lineages cannot keep up. This led Glesener & Tilman [2] to formulate their verbal biotic interaction model, where the distribution of parthenogens in marginal habitats is explained by the lesser parasitism, competition or predation they experience there (note that while they did not use the word 'marginal', their list of characteristics of habitat matches those discussed in §1a). When the need to constantly adapt is removed, asexuals outcompete sexual lineages. An intriguing aspect of this hypothesis is the complex identity of 'marginality': it first assumes that marginal habitats are generally difficult to persist in, as this is clearly required to explain the absence of parasites, competitors or predators; thereafter, for those few species that do succeed there, life can become 'easier', i.e. requiring less continual adaptation, than it was in the core habitats. The gradient assumed here is that from core to marginal habitats, the selection pressures shift from biotic to abiotic.

While much of the Red Queen literature, being vast, is beyond the scope of this review, it is noteworthy that in some cases, there is geographic variation in the prevalence of parasites, and rates of sex have been shown to be indeed higher in parasitized zones (e.g. freshwater snails [111]; plants [4]; see also [112] for analogous results with outcrossing versus selfing). But as noted in §2d, asexuality can present itself as a genetically diverse array of asexuals, and such a coexisting set can be as well equipped to deal with parasitism as a sexual population, given alternating frequency-dependent selection that acts on the different clones [106].

The second prerequisite for a Red Queen interpretation of geographic parthenogenesis is that biotic interactions decrease with latitude. This was firmly thought to be the case for a long time, until recent meta-analyses over large geographic scales yielded conflicting results ([113], versus [114,115]). However, some authors argue that such broad-scale studies will miss the relevant patterns occurring within species [116], as, for instance, the latitudinal gradient in plant–enemy interactions documented in the dandelion, a textbook example of geographic parthenogenesis [4].

Resource competition is another context where sex is expected to be beneficial. The Tangled Bank hypothesis and its variations [18,117] propose that the phenotypic diversity of sexuals enables them to share the resource space more efficiently than a homogeneous array of clones interfering with each other's success. This idea has led to the expectation that sexuals should prevail in habitats with diverse and structured resource, whereas the benefits of diversity vanish in simple habitats where all compete for the same resource, allowing asexuals to express their demographic advantage. The argument extends to habitats where disturbances are so frequent that they cannot develop much structure [18]. This is, again, in line with a vision of parthenogens as fugitive species [25]. Note that the above line of thought requires sexuals to be the more diverse population (see §1b).

Resource diversity appears to have been the only idea to receive a substantial amount of modelling attention in the specific context of geographic parthenogenesis (table 1). Gaggiotti's model [23] assumes a coarse-grained environment (each individual experiences one type of resource) with dispersal between patches, and predicts persistence of either sexuals or asexuals depending on intra- and inter-specific competition coefficients. His model does not explicitly include genetic diversity, but outlines the rules of competitive interactions that allow for the persistence of each type. In biological terms, asexuals win when the diversity of resources is low (as everyone competes for the same thing), or when sexuals have a diversity low enough to lose their competitive advantage. Another series of papers [73,74] explore the idea that sexuals benefit by being able to exploit underused resources. Resource use is determined by the match between genotype and environment, and the models explore how sexuals may be better at finding underused resources because offspring are not clones of their parents (shown for a single habitat [73]; multiple habitats along a one-dimensional gradient [74]). To simulate a change from the centre to the boundary of the species range, Song *et al.* [74] impose a gradient in terms of death rate, variety of resource types and/or resource regrowth rate. They find that asexuals (with the demographic advantage of no male production) are favoured by small population sizes, high death rates and high resource growth rate, all of which decrease competition, as well as by the availability of fewer resource types. These factors all reflect their core assumption that sexuals' diversity allows them to use resources that would otherwise remain unused.

The above-mentioned models tend to assume, implicitly or explicitly, that asexuals exhibit lower phenotypic diversity than sexuals. It should also be kept in mind that the diversity within a reproductive mode can also depend on location: in a broad meta-analysis of 115 species of animals and plants (regardless of their reproductive mode), Eckert *et al.* [118] found a decline in the diversity of neutral genetic markers towards the range margin in 64% of the studies they reviewed. Caution has to be exerted when extrapolating from neutral to non-neutral diversity [119], and the adaptive microniche variation on which relies the Tangled Bank hypothesis might be more resistant to drift than neutral markers; however, a parallel decrease in polymorphism can still be expected, especially with a population history of founder effects.

Finally, stability of the environment has received attention as an explanatory factor (see also §2d), but it is currently difficult to judge to what extent this explains geographic patterns. Not only is it challenging to provide generalizations about whether marginal habitats are less stable than core habitats: some habitats can vary much but do so in a relatively predictable manner (seasonality). In addition, asexuals have been predicted to fare better in either stable or unstable habitats, depending on the definition. Stability has been argued to favour them because of their inability to adapt otherwise (theory [105]; empirical evidence [120]). But unstable environments have likewise been argued to favour asexuals, either because they are a general-purpose genotype (see §2d) or because of an idea rooted in the r–K selection literature: environmental variation selects for fast growth rates (potentially achieved by avoiding the costs of sex) over competitive abilities ([10,18] and empirical evidence [121]). The relationship between environmental stability, predictability and the prevalence of sex appears to be an area of much potential for future work, especially because species with facultative sex provide additional hints. Asexual life cycles of such species typically go on as long as conditions remain relatively unchanged, whereas deteriorating conditions lead to sex (e.g. cyclical parthenogens have sexually produced resting eggs that can withstand winter and/or drying out [122]). Theoretical work in this area appears lacking, whereas empirically Schmit *et al.* [29] showed in *Eucypris* clams that pond hydroperiod mattered less than predictability in explaining the presence of asexuals.

(f) The importance of gene flow

Sexual species can experience variations in gene flow and heterozygosity in a manner that has no direct analogy in parthenogenetic lineages (genes of course do 'flow' if parthenogens migrate from one area to another, but they do not enter new genetic backgrounds in the process). This has several potential consequences for geographic parthenogenesis.

Insufficient gene flow can lead to inbreeding depression, brought about by small population sizes or genetic bottlenecks. These are characteristic of invasion of new environments or metapopulations dynamics, with cycles of extinction and recolonization. In those contexts, apomictic parthenogens can be particularly good colonizers, as they travel with 'frozen' levels of heterozygosity, and can also benefit from reproductive assurance and high growth rate in the absence of strong competition [21,22].

Asexuality also provides protection against outbreeding depression. For instance, mating with immigrants can result in the loss of locally adaptive alleles [123]; see [124] for the only evaluation so far of outbreeding depression in a context of geographic parthenogenesis, but with inconclusive results. This is problematic in the context of asymmetric migration from a source to a sink environment. The matter is complex, however, because gene flow from the core to the margin can either facilitate adaptation of sexuals by increasing the genetic variance for selection to operate on, or impair it because of core-adapted genes swamping any local adaptation [125,126]. To what extent asexuals can achieve local adaptedness depends on the frequency of transitions: if sexuality regularly gave rise to new asexual lineages, some of them might be based on the locally best genotypes which they can then retain better than the sexuals; but if transitions to asexuality are rare (and if they first have to overcome problems with perfecting an asexual life cycle [127]), and asexuals have to reach new areas by dispersal instead of being newly created at the local site, achieving local adaptation via asexual means can be much harder.

Peck *et al.* [24] built a model of outbreeding depression based on a landscape with an environmental gradient, where individual fitness depends on the degree of match between phenotype and environment, in the presence of short-distance dispersal as well as mutation (a mutation is required to create the first asexual individual; further mutations potentially enable its descendants to adapt locally). Population productivity is set to decline from an area called 'south' to the 'north', which yields asymmetric gene flow and prevents northern individuals from fully adapting to their environment (gene swamping). The model is able to produce a pattern where the north eventually becomes populated by locally adapted asexuals, which maintain higher fitness than sexuals by escaping the swamping. Peck *et al.*'s assumptions of a very large (threefold) difference in productivity between the core and the margin likely contribute to the neatness of the pattern, but outbreeding depression preventing local adaptation is a reality in the wild [125]. In an alga, Lagator *et al.* [126] showed experimentally that both sex and migration on their own were beneficial in helping a sink population to adapt, but that asexuality did better than sexuality in the case of high immigration rates, by preventing outbreeding depression.

Lack of recombination might be a short-term benefit, but it becomes a problem for asexuals in the long run, which adds a temporal dimension to the above results. Muller [128] pointed out that deleterious mutations fixing at a higher rate in the absence of recombination are a particularly severe problem for asexual lineages. This mutational meltdown will decrease their fitness compared with sexuals (Muller's ratchet). Space interacts with time to play a role in determining whether an asexual lineage with a demographic advantage will succeed in displacing a sexual parent before its fitness is decreased too much ([129] and references therein).

In this race against the clock, any factor that slows down the spread of asexuals makes their fixation less likely. Salathé *et al.* [75] modelled a situation where asexuals, in principle, have a superior growth rate, but because of short-range dispersal they compete essentially among themselves. This prevents them from realizing fully their advantage and slows down their invasion (table 1). Invading a large sexual population may therefore prove too much of a challenge for asexuals: they will eventually accumulate too many mutations before the invasion is complete, and the process ends with asexuals being outcompeted by sexuals. Salathé *et al.* [75] state that their model fits patterns of geographic parthenogenesis if one takes small population size as a characteristic of marginal habitats, as it is faster to invade a small than a large population. Note, however, that despite an explicit spatial model being included in their paper, it does not produce a spatial gradient from sex to asex; instead, the pattern is the fixation of either, depending on parameter values. We suspect that showing simultaneous persistence of reproductive modes in different regions of the simulated world might require extending the spatial scale such that the dynamic processes can occur relatively independently in different parts of the world.

In another model featuring metapopulations, this time with clear between-deme structure, Hartfield *et al.* [129] repeat many findings of earlier work (high levels of subdivision, with low migration and genetic flow between the demes, make asexual spread slow), and additionally connect the findings to explicit predictions of F_{ST} levels. They show that sex is maintained at the metapopulation level only for high levels of F_{ST}.

While the models discussed here have not explicitly sought conditions of stable geographic patterns of parthenogenesis (the emphasis being on predicting which reproductive mode will eventually reach total fixation in the landscape), the outcomes often suggest that fixation over a large scale needs a long time. Given how little is known about the long-term stability of geographic parthenogenesis (see §2c), such outcomes are not irrelevant, and some published models give explicit temporal dynamics (see e.g. fig. 4 in [75]).

Interestingly, invading a large population of sexuals can prove difficult, but once established, a large population of asexuals should resist mutational meltdown (and extinction) longer than a small one. Ross *et al.* [130] found that in scale insects, asexuality is more common in polyphagous, pest or widespread species, and turn the traditional causal argument around: instead of explaining their distribution by their reproductive mode, they propose that species that produce very large populations in the first place resist Muller's ratchet for longer, thus remaining observable today. In support of this direction of causation, they also report that sexual species of genera containing parthenogens have relatively large geographic ranges. These two predictions, that asexuals should be able to invade small populations better, but to persist in large ones better, highlight the importance of the time scale of invasion and persistence of asexuals (see also §2c). They also provide additional reasons why the most favourable scenario for asexuals is to colonize a new environment: there, no sexual competitors will slow them down, nor outcompete them once mutational meltdown has reached critical levels (see also §2a).

How much is known empirically about the above models' assumptions regarding inbreeding and outbreeding depression, metapopulation dynamics and mutational meltdown? In a review of sexual species' range limits over a broad taxonomic scale, Sexton *et al.* [28] found mixed support for marginal populations being smaller or exhibiting lower fitness or density. Gaston [131] in his review of the literature finds stronger support for systematic core-to-edge variation in levels of occupancy than in local population density or size. Once more, it would be invaluable to monitor the contemporary spread of asexual species, and possibly the recovery of sexuals, and gather data on population dynamics, structure and on chronology.

(g) Synthesis of the hypotheses

Geographic parthenogenesis does not occupy the centre of the stage when it comes to theoretical questions surrounding sex.

Perhaps it should, given that it is discussed as one of the few settings to provide repeatable clues as to which of sex or asex wins (though, as §2b shows, the identity of the causal factor behind it can be difficult to disentangle from the various covariates). The enigma of why sex persists at all has received much more attention. Theoretical work has identified ecological parameters that are thought to favour sexual reproduction, ranging from the presence of coevolving parasites (Red Queen [2]) to the complexity of the environment (Tangled Bank [23,73,74]) or its temporal unpredictability [105]; see [110] for a recent review. Any model where one parameter impacts the likelihood that sex is maintained can predict repeatable patterns of geographic parthenogenesis, if this key parameter correlates, in some systematic way, with geography. However, this step remains largely untested. There seems to be no way to avoid the difficult task of going beyond simple geographic mapping of sexuals and asexuals, and of characterizing in detail the ecological niche and population processes at play in their respective ranges (including what happens at any range overlap).

3. Future directions

Geographic parthenogenesis is an 'old' research topic that could be revived using a multitude of approaches. We present a non-exhaustive list of ideas in table 2 and discuss below the rationale and potential pitfalls in developing such a research programme.

(a) Better documentation of the patterns

The concept of geographic parthenogenesis primarily refers to species where both a sexual and an asexual form exist and are geographically more or less distinct [1]. However, the term has been taken by some authors to specifically refer to species, or pairs of sister species, where parthenogens are found in wider areas, higher latitudes, altitudes, disturbed areas or island-like habitats, considered typical patterns. What appears to be largely missing is a quantitative characterization of sexual and asexual ranges that is done in a systematic way, avoiding pre-selecting species based on an interesting pattern already being noted. Whether a case study matches an expected pattern is open to subjectivity, and a statistical validation of the soundness of the suspected trends is therefore desirable.

Plants appear better studied than animals in this respect. Bierzychudek was the first to test whether parthenogens span larger and colder ranges than their sexual counterparts [5]. She examined 43 cases (10 genera) of plants where the distribution of both forms was known: in 76% of cases, the asexuals' range was larger and more northerly. She also compiled data of 130 sexual and asexual species regarding whether they occupied a previously glaciated area or not. Significantly more sexual species were found only in non-previously glaciated areas, and more asexuals were found only in previously glaciated areas.

While Bierzychudek's study was based on precise distribution data and statistical testing, caveats need to be mentioned. The species constituting the dataset did not satisfy assumptions of random sampling across families as they were imposed by the availability of data, leading to a strong taxonomic bias: more than half of included cases are from the well-studied Asteraceae that contain a high proportion of apomicts [41], and happen to harbour almost all the angiosperms with autonomous, rather than pseudogamous, parthenogenesis [140]. Thus, we can conclude that geographic parthenogenesis appears to be a consistent pattern in autonomous Asteraceae, but patterns in pseudogamous angiosperms have not been investigated in detail [140].

Since the work of Bierzychudek [5], no broad-scale quantitative test has been published to validate the assumed typical differences in the range size, localization and properties of sexuals and asexuals (though note the valuable study of Grossenbacher *et al.* of the equivalent question in selfing plants [38]; see §2c). The geographic parthenogenesis literature has clear 'favourite taxa': temperate angiosperms with distributions in Europe and northern America, lizards [27] and Coleoptera [141]. Reviews can be found on plants and animals in [8], on angiosperms in [140], on arthropods in [17]. Expanding the discussion to other groups is crucial to determine if asexuality affects distribution patterns universally and in a consistent fashion (a best-case scenario, because then geographic parthenogenesis could give the crucial clue to the mystery of the persistence of sex as a whole), or if recurring geographic patterns are merely a quirky phenomenon restrained to a few groups. In the latter case, it could heavily interact with ecological specificities of these groups to explain the distribution of their asexual forms (as already pointed out in [10,19,130]). For instance, Asteraceae are widespread exploiters of pioneer habitats [142].

The enormous group of internal and external parasites is remarkably absent from the debate (though their sexuality is not always straightforward to assess [143]). Sexual reproduction is commonly viewed as a way to keep up with parasites, but how parasites might keep up with their hosts is less often discussed. Successful and widespread species of asexual pathogens exist [144], but to the best of our knowledge, they have not been compared with sexual sister taxa in any geographic context. Being an agricultural pest has also been shown often to be associated with parthenogenesis [12,130]. Some globally spreading pest species of fungi are known to use only vegetative reproduction outside their native range, where they are normally only facultative asexuals, despite several independent introductions being documented [43].

Finally, §§1 and 2 emphasize that current explanations for geographic parthenogenesis patterns tend to be based on ideas about the emergence, invasion and demographic nature of asexual lineages that cannot all be shared by existing asexual lineages. To identify which of these candidate explanations are most relevant, it would be extremely valuable to document how well model assumptions match the properties of each category of parthenogens, and whether some categories are more strongly associated with a given geographic pattern. For instance, a database such as the tree of sex [133] provides a good starting point for cataloguing species where both sexual and asexual populations are found, their respective distribution, and candidate characteristics to explain geographic patterns (ecology, ploidy, hybridity, type of asexuality…). Given the tremendous amount of biogeographic data now available, fine-scale geographic analyses could also prove useful, as would filling in the gap between the time since the last glacial maximum and much more ancient processes (see [145] for arguments why this could be important).

While addressing these goals is clearly beyond the scope of this review, it is instructive to lay out some of the pitfalls that

Table 2. A list of suggestions for future research. (GeoP, geographic parthenogenesis; GPG, general-purpose genotype; FNV, frozen niche variation.)

what needs to be done	why?	state of the field
broad-scale patterns: quantify and statistically compare geographic distributions of sexuals versus asexuals over a wide phylogeny (range, latitude, habitat type)	patterns still need to be validated. Do they give us universal information about contextual benefits of sexual versus asexual reproduction, or are results taxonomically restricted and/or idiosyncratic?	— some meta-analyses already exist: selfing plants [38], scale insects [130], pests [12] — new developments in functional biogeography [132] could include intra- and interspecific variation in reproductive mode
broaden the taxonomical scope and form a database of parthenogens' characteristics (ecology, autonomous reproduction, heterozygosity protection, polyploidy, hybridity. . .); include selfing and vegetative reproduction and traits of sexual sister species (or taxa)	find out if geographic patterns associate mostly with certain characteristics of asexuals, over a wide range of organisms. Does the absence of sex itself matter, or rather its correlates?	— tree of sex [133] is a starting point — [59] outline how research could benefit from comparing different genetic consequences of various parthenogenesis systems across sister species and taxa
document the genetic diversity of asexuals and their sexual counterparts	a diverse assemblage of clones, or the possibility of cryptic sex, can perform as well as sex in ecological times. Models sometimes assume asexuals are more diverse, sometimes less. Only parthenogens surviving with little diversity can tell us about contexts where sex is not necessary [59]	— new molecular methods make genotyping increasingly easy, as well as detection of rare sex signatures — e.g. early reviews: genetic diversity in asexual reptiles [27]; comparison of sexual versus asexual mitochondrial genetic diversity available in 10 systems [134]
identify evidence for different stages of asexual or sexual spread; document the temporal dynamics of contact zones and boundaries	if the range of the sexual species shrinks, asexuals may be showing their demographic advantage, or asexuality may be contagious if asexuals spread beyond the sexual range, this is indicative of better colonizing abilities or broader niche (via FNV, GPG, hybridity, polyploidy. . .) if the asexual range shrinks, they may have been faster colonizers but sexuals are catching up; or they may display decreased fitness from mutational meltdown	temporal dynamics of sexual/asexual systems are still little known, apart from indirect inferences based on some habitats not having been available for very long
small-scale patterns: niche characterization of overlapping sexuals versus asexuals; displacement and competition experiments; experimental evolution	coexistence or competitive exclusion experiments will inform us whether the experimentally created ecological conditions favour sex or asex; if multiple conditions are tested and their geographic distribution is known, studies will link ecological patterns behind geographic parthenogenesis to the general theories of sex	examples: ostracods and predictability [29], woodlouse and abiotic preferences [135], dandelions and plant–enemy interactions [4]. Many experimental evolution studies on sex exist, but conditions of experiments have typically not been interpreted in ways that make potential links to the geography of natural populations clear
existence of geographic clines between sexual core and contact zone with asexuals with respect to important characteristics of the population or its environment (population size, genetic diversity, biotic interactions, resource structure. . .)?	many general theories for the maintenance of sex can lead to GeoP if there is a geographic trend in its parameters, but this needs testing	recent meta-analyses about latitudinal reduction in biotic interactions ([113] versus [114,115]) or core to margin genetic diversity decline [118]. Applied to GeoP systems: [4]

(*Continued*.)

Table 2. (*Continued.*)

what needs to be done	why?	state of the field
document mating interactions between sexual males and parthenogenetic females; find evidence for sperm or pollen limitation	reproductive assurance might boost the spread of asexual organisms if mate availability is limiting. On the flipside, sexual conflict predicts that it is in the male (but not always in the female) interest to have females reproducing sexually. If population density is high, sexual harassment by males is a more severe problem for females, and if this leads to more frequent sex this can turn facultative sex into a pattern of geographic parthenogenesis via effects of local population density [136]. Finally, neutral hypothesis for geographic parthenogenesis would get support from deleterious hybridization	examples of spatial reproductive assurance studies in plants: [137–139]. [136] provides a theoretical basis of the conflict idea
develop theory more systematically; stop treating geographic parthenogenesis as a 'separate' topic from the rest of the theoretical literature on sex	many hypotheses presented in this paper exist in the literature as verbal ideas only. General models on the evolution of sex miss out on opportunities to test them if they do not phrase their predictions in contexts where geography might covary with parameter settings	table 1 contains a list of what already exists

would have to be avoided. One tends to assume that reproduction is sexual until proven otherwise (indeed, it was the curious scarcity of males that led Vandel on the right track [1]), and detection of asexuality might happen far more easily when the asexual range is large than when it is small—particularly if asexual and sexual forms overlap in range. Occurrence of asexuals in 'human-associated habitat' is prone to another detection bias. The only species of snake known to be obligately parthenogenetic is the fossorial species *Ramphotyphlops braminus*, also called 'flowerpot snake' after its worldwide introduction along the global potted plant trade [146]. Here, it seems reasonable to assume that a closer look at its reproductive system was encouraged by it is cosmopolitanism and association with humans. This kind of detection bias has to be considered when arguing for a causal relationship between parthenogenesis and association with humans (see [27]).

Another factor to consider is potential nonlinearities in data: in a recent field survey, the relationship between altitude and parthenogenesis in plants proved not as straightforward as previously thought, as above the altitude where asexuals increase in frequency, sexuals may take over again [147]. Finally, there is the problem already mentioned in §1a: how to deal with the proliferation of environmental patterns claimed to exist. For instance, the claim that asexual populations tend to inhabit more arid environments than sexuals, is documented mainly in species of the Australian desert [6,8,148]. As with the 'high latitude' pattern, drier habitats of the parthenogens might just reflect the direction the climatic envelope moved, opening new areas to colonization. There are also subtle differences in how the question has been asked, with consequences for the characterization of the pattern. Rather than showing that parthenogenetic sisters occupy consistently drier habitats than their sexual sisters, the data suggest that the desert harbours more asexual taxa (along with their sexual counterparts) than other Australian environments [6,149].

(b) At what scale are we expected to find the pattern?

Should the distribution of asexual and sexual forms be different enough that a satellite could, in principle, map these? If we require this to be the case, then interesting causalities might remain hidden. For instance, Fussey found that sexual woodlice associate with more calcareous microhabitats than their asexual counterparts, but the scale of such environmental variation, being very small and patchy, led to no identified pattern of geographic parthenogenesis [135].

Bell used 'ecological parthenogenesis' to refer to environments or lifestyles for which the incidence of parthenogenesis is higher or lower than average for a given clade [18, p. 311] (e.g. in agricultural environments [12]). Reality may offer us a continuum from small-scale habitat preferences and/or outcomes of competition, to large-scale patterns. For instance, all known examples of parthenogenesis in tardigrades involve freshwater, and not marine, species [150]. Similarly, parthenogenesis is common in non-marine ostracods [18], but only one marine species has so far been confirmed to be parthenogenetic [151]. In the Baltic Sea, which offers a wide gradient of salinity, several normally strictly sexual algae reproduce solely by vegetative propagation in freshwater areas [44,152]. An explanation is that gametes, having evolved in seawater, face osmotic problems in freshwater, which could favour a switch to asexual reproduction [153]. Another hypothesis considers the marine environment to be more stable with more biotic interactions, whereas freshwater systems pose fluctuating selection pressures—but even if such a generalization were justified, as we highlighted above (§2e), there are difficulties in predicting which way this should impact sex. For instance, parthenogenetic mites and springtails tend to inhabit the stable soil horizon, while sexuals dwell above, in the more variable litter [154,155]; somewhat frustratingly, earthworms show the opposite pattern [156].

If sex and asex are each favoured in different ecological conditions, then large-scale patterns of geographic parthenogenesis are analogous to small-scale patterns of 'ecological parthenogenesis', only organized over a wide geographic gradient. Alternatively, large-scale patterns can stem from large-scale events such as glacier retreat. Integrating data from organisms of all sizes and on various spatial scales might be a key step in disentangling the causes of geographic variation in reproductive mode. We also emphasize that 'marginal' and 'geographic' are human constructs based on scales that are relevant for us, and those concepts have to be carefully adapted to the reality of the studied organisms.

4. Conclusion: mind the diversity!

The dazzling differences among cases of parthenogenesis, their putative habitats and reasons why they are there, are poorly reflected in current modelling efforts. Despite the theoretical attachment to a twofold cost of sex, empirical estimates and more detailed theory point towards frequently lower costs in the wild [45,157], and mathematical modelling of geographic parthenogenesis should incorporate some flexibility and realism in this parameter (table 1). The twofoldness of any cost is based on certain assumptions about the role of males [45], yet it is noteworthy that apart from one reference in table 1 [76], males (or male function) are not considered. Their behaviour towards parthenogenetic females, or intralocus sexual conflict, could have important consequences [158].

Another noteworthy point is that all models of table 1 explicitly or implicitly concern autonomous parthenogens, though some results could probably be extended to pseudogamous cases whenever coexistence is possible, or self-fertilization. Apomictic parthenogenesis appears to be a necessary requirement for only one of the models of table 1 [24], but it is currently unknown whether automixis would shift each model outcome towards an asexual disadvantage (it is an extreme form of inbreeding), or whether the benefit of freezing favourable adaptations would be of overriding importance. Because the way the zygote is produced determines how the actual genetic benefits of sex arise, assessing the ecological and evolutionary success of parthenogens with different reproduction modality is especially relevant (see [59] for suggested research avenues). Verbal models also display a tendency to build scenarios tailored to one particular category of parthenogen and pattern. There appears to be much to be gained if we remember to celebrate the diversity of how and where asexuals appear and persist, both theoretically and empirically.

It also appears timely to connect the geographic parthenogenesis literature much better with related questions. We have already highlighted how, if patterns prove consistent with one explanation but not others, we could gain much in terms of understanding sex in general. Other 'neighbouring' fields include the ecology of selfing organisms, which offer similar geographic trends (§§1b and 2c) while sharing another trait with parthenogens: the twiggy nature of their phylogenetic distribution, and an unfortunate reputation of being evolutionary dead-ends (but see [159,160]). Studies of vegetatively reproducing organisms are also largely disconnected from other forms of asexuality, and papers reporting a latitudinal decrease in the use of sex and increase in vegetative reproduction often propose idiosyncratic explanations, without linking it to the general literature on geographic parthenogenesis [161]. Vegetative reproduction is also interesting because it poses strong constraints on dispersal distances—though this did not prevent the Mediterranean Sea from being colonized by a single, vegetatively reproducing genotype of seastar, which remarkably also happens to be a male [162]!

The study of invasion dynamics and range expansion are particularly relevant for geographic parthenogenesis. First, because asexuality is frequently found in the non-native range of invasive species, and second, because some of the conditions we discussed here as potentially favourable to asexuality can be found at the edge of an expanding population: enemy release, low density of mates, inbreeding and low diversity of sexuals [163]. To date, no model of geographic parthenogenesis has focused on how well asexuals would do on the front of an expansion (but see Peischl *et al.* for a first step in that direction [164]). Finally, there is a large body of work on local adaptation and its coevolution with dispersal [165,166], but intricacies of sex are rarely discussed in this context (but see [126]); taxa with sexual and asexual forms could also offer much insight into this question.

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