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DIVERSIFICATION IN SEXUAL AND ASEQUAL ORGANISMS

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Abstract.—Sexual reproduction has long been proposed as a major factor explaining the existence of species and species diversity. Yet, the importance of sex for diversification remains obscure because of a lack of critical theory, difficulties of applying universal concepts of species and speciation, and above all the scarcity of empirical tests. Here, we use genealogical theory to compare the relative tendency of strictly sexual and asexual organisms to diversify into discrete genotypic and morphological clusters. We conclude that asexuals are expected to display discrete clusters similar to those found in sexual organisms. Whether sexuals or asexuals display stronger clustering depends on a number of factors, but in at least some scenarios asexuals should display a stronger pattern. Confounding factors aside, the only explanation we identify for stronger patterns of diversification in sexuals than asexuals is if the faster rates of adaptive change conferred by sexual reproduction promote greater clustering. Quantitative comparisons of diversification in related sexual and asexual taxa are needed to resolve this issue. The answer should shed light not only on the importance of the different stages leading to diversification, but also on the adaptive consequences of sex, still largely unexplored from a macroevolutionary perspective.

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It is widely agreed that species are fundamental units of life. But why do species exist? Why does life fall into discrete clusters with respect to genotype, morphology, and behavior, rather than forming a continuous distribution? Coyne and Orr (1998) called this “one of the most important but neglected questions about speciation” (p. 287) and cite two main general explanations proposed by Maynard Smith and Szathmari (1995):

(1) Species arise by divergent selection leading to adaptation to different ecological niches. There is increasing experimental and theoretical support for ecological speciation in sexual organisms (Schluter 2001) and it has frequently been invoked to explain speciation in asexual organisms (Fisher 1930; Mayr 1957; Hutchinson 1968).

(2) Speciation is a consequence of sexual reproduction. Sexual reproduction (with at least some outcrossing) maintains cohesion within populations, whereas reproductive isolation of different genotypes or populations leads to divergence and speciation (Mayr 1957). Maynard Smith and Szathmari (1995) and Coyne and Orr (1998) regarded this hypothesis as most important, but they highlighted that empirical tests were scarce.

One way to distinguish the importance of ecological niches and sexual reproduction might be to test whether asexual organisms fall into discrete clusters to the same extent as sexual organisms. If they do, it would suggest that sex is not necessary for the formation of discrete clusters. Taxonomic evidence appears to support this in some groups. For example, in the famously asexual bdelloid rotifers there are often clear morphological differences among described spe-

cies, qualitatively similar to those found in sexual groups (Hutchinson 1968), and taxonomists have identified species more consistently than in sexual monogonont rotifers (Holman 1987). Moreover, bdelloids fall into distinct clades based on mitochondrial gene sequences (C. W. Birky, unpubl. data). These results show that clusters can form in asexual organisms, but not how effectively. More satisfying would be a quantitative comparison of the pattern of diversification between sexual and asexual clades. Such studies have not yet been made, but are likely to appear soon (Barraclough and Nee 2001).

Before performing such studies, it is vital to consider the expected effects of presence or absence of sexual reproduction on patterns of diversification. Previous accounts have made general statements but there have been few detailed treatments. For example, recombination tends to oppose genetic divergence within populations, by eroding associations across multiple loci (Felsenstein 1981). Without compensating benefits, therefore, genetic divergence might be harder in sexuals than in asexuals. Moreover, the comparison between sexuals and asexuals is complicated by the difficulty of applying a consistent species concept. The biological species concept cannot apply to asexual organisms because all individuals are reproductively isolated entities. Attempts have been made to devise a universal species concept that will be widely accepted, but the literature bears witness to the difficulty of this endeavor (Mishler and Donoghue 1982; Hey 2001).

Here, we present a critical account of how sex versus asex is likely to affect the tendency of lineages to diversify. To

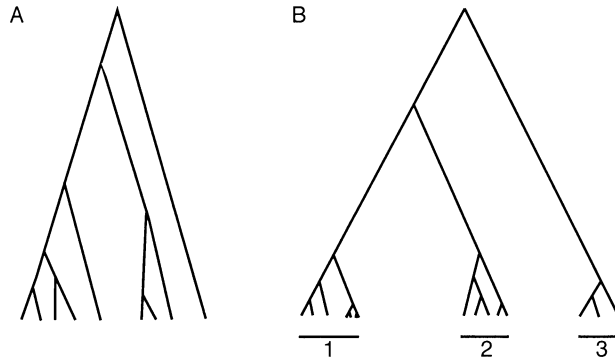


FIG. 1. Hypothetical gene trees. (A) A gene tree from a single population. (B) A gene tree showing the existence of three discrete clusters on the end of long stem branches.

avoid problems with defining species, we focus instead on comparing patterns of genetic and morphological diversification between sexuals and asexuals. Our framework is to consider expected gene trees under alternative scenarios. This approach provides a link between pattern-based surveys of genetic and morphological diversity and the population genetic processes underlying the observed patterns. After considering the patterns of diversity expected in single populations in simple environments, we compare the relative response of sexual and asexual populations to conditions favoring diversification. Finally, we discuss likely confounding factors that differ between sexual and asexual clades beyond the presence or absence of recombination.

GENE TREES: BACKGROUND AND DEFINITIONS

A gene tree is a representation of the ancestry of alleles from the same locus sampled across a set of individuals. Under the simplest null model that the individuals can be treated as a random sample from a single population, the expected gene tree conforms to the genealogy for a single population (Fig. 1A). For example, if a locus has evolved under a neutral model, the expected tree would be the neutral coalescent (Kingman 1982; Hudson 1991). The expected gene trees for a fairly wide range of conditions are known, including changing population size and various selection regimes (Hudson 1991; Neuhauser and Krone 1997; Fu and Li 1999). From this, we can predict expected patterns of genetic variation in a population, and thereby predict expected variation in morphology and other traits.

We first consider gene trees for a single population with a constant size of N individuals, which is either entirely sexual (with random mating) or entirely asexual. For present purposes we do not consider partial or rare recombination (e.g., bacterial speciation, Cohan 1998; Cohan 2001). We begin with a haploid model for simplicity, discussing the effects of diploidy later. Hence, in both the sexual and asexual populations, for a single locus there are N genes in the population at any time. Our account is based primarily on work assuming the Fisher-Wright model, namely that generations are discrete and that the genes present in an offspring generation were obtained by sampling N genes with replacement from the parent generation. However, we believe the general points are qualitatively robust to other formulations. One

property that we will focus on is the time to most recent common ancestor (*Tmrca*). This is the time back from the present at which the gene tree coalesces to a single common ancestor for all genes in the sample.

Our main interest is in the formation of discrete clusters beyond levels expected under simple null models that individuals come from a single population. By clusters, we mean groups of individuals with similar genetic and/or morphological characteristics, separated from other such groups by gaps in genotypic/morphological space. Classic accounts have visualized clusters as peaks in the n -dimensional frequency distribution of morphological traits (Hutchinson 1968). In the context of gene trees, discrete clusters are apparent as clumps of terminals on the end of long internal branches (Fig 1B). Importantly, we are interested in clusters found consistently across multiple loci, for example, in surveys of several DNA markers. A few loci may not cluster in the same way, for example, due to ancestral polymorphisms or lack of variation, but overall we require the expected population genealogy to exhibit clusters, not just a given gene tree (Avice 2000). For now, we consider idealized gene trees, that is, knowledge of the true genealogy of a locus.

GENE TREES IN A SINGLE POPULATION, NO DIVERSIFYING SELECTION

Neutral Case

The expected gene tree for a single locus under a neutral model is given by neutral coalescent theory (Kingman 1982; Hudson 1991). For a haploid population, *Tmrca* is exponentially distributed with expectation $2N(1-1/k)$ generations, in which k is the number of genes sampled in the gene tree. Hence, for large samples, the expected time until all genes in the sample coalesce is approximately $2N$ generations. This is the same for haploid sexuals and asexuals. The expected *Tmrca* would be doubled in a diploid sexual population because a diploid population harbors twice as many genes.

The difference between haploid sexual and asexual populations is apparent when we consider gene trees across multiple loci. In asexuals, there is no recombination, therefore all loci have the same gene tree. Hence, there exists a tree structure with recognizable clades that differ by varying amounts from other such clades (Fig 2A, Higgs and Derrida 1992). This leads to inherent discreteness within asexual populations simply as the result of stochastic individual replication. In the sexual case, although each locus has a gene tree similar to a single locus in the asexual case, gene trees differ among incompletely linked loci (loci show different realizations of the random process). Hence, there is no tree structure within the sexual population because the overall genotype comprises the average of the set of different random gene trees (Fig 2B). Sexual populations should display a unimodal distribution of neutral genetic or morphological variation based on multiple loci, without the hierarchical variation and gaps expected in an asexual population (Higgs and Derrida 1992).

Selection against Deleterious Mutations

For a locus experiencing selection against deleterious mutations arising at a constant rate, the expected gene tree is

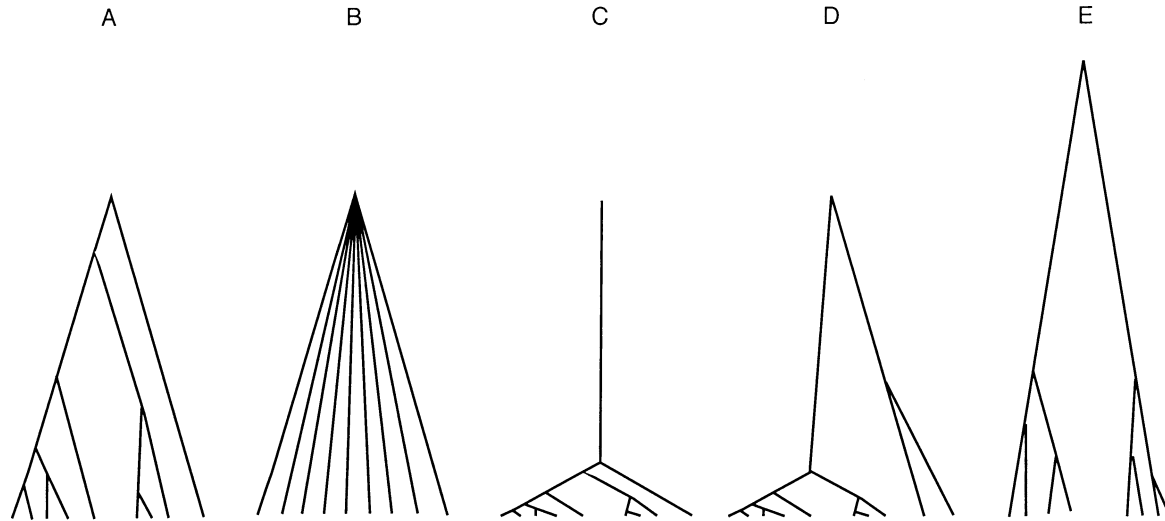


FIG. 2. Hypothetical gene trees for single populations under a range of scenarios. (A) Neutral coalescent for a single locus in a haploid population. The same tree is expected for a consensus tree of multiple loci in asexuals, assuming neutral coalescence. (B) Consensus tree for multiple loci in a sexual haploid population. The polytomy reflects incongruence among unlinked loci. (C) Gene tree following completion of a selective sweep that occurred at the locus or linked loci. (D) Gene tree sampled midway through a selective sweep. (E) Frequency-dependent selection at a single locus. The two clusters represent the two alleles favored by selection.

very similar to the neutral coalescent. High and low selection coefficients have little effect, but intermediate selection coefficients reduce the *Tmrca* slightly below $2N$ generations (Neuhauser and Krone 1997; Przeworski et al. 1999). Background selection at loci linked to the region of interest could have the same effect, and this is likely to be stronger in asexuals because the entire genome is linked. However, the qualitative comparison of sexual and asexual populations is unchanged from the neutral case.

Selective Sweeps

The spread of a beneficial variant through a population tends to homogenize variation at linked loci, referred to as a selective sweep (Fig. 2C, Barton 2000). Sweeps occurring within, on average, the last $2N$ generations will reduce the *Tmrca* of a gene tree to the time since the sweep began (Galtier et al. 2000). In asexuals, a selective sweep homogenizes the entire genome. In sexuals, a single sweep only homogenizes the part of the genome that is tightly linked to the beneficial variant. Multiple sweeps can occur at the same time but will rarely homogenize the entire genome. Once a sweep is finished, the expected gene trees return to those for the neutral model.

The effect of sweeps on surveys of genetic and morphological diversity will depend on their frequency. If sweeps occur rarely, then most populations we sample will be unaffected and the qualitative pattern of variation will be similar to the neutral case. If sweeps are frequent, some populations will be sampled during a sweep or recovery from a sweep. In this case, an asexual population will display a single strong cluster of individuals, those with the new variant within a wider tree (Fig. 2D, Barton 2000). No such pattern would be expected for multilocus measures in sexuals because sweeps would only affect regions linked to the selected locus. Finally, if a change in environment leads to sweeps at multiple loci, sexuals are likely to evolve faster towards the new op-

timum (assuming the rate of origin of beneficial alleles is not limiting, Barton and Charlesworth 1998; Burt 2000), perhaps increasing the chance of catching asexuals during a sweep.

Conclusions

Within a single population in a simple environment, asexuals display a hierarchical pattern of variation, in contrast to the unimodal distribution expected for multilocus traits or measures in sexual populations. The broad pattern is unaffected by selection against deleterious mutations or selective sweeps. This tree-like ancestry could give the appearance of discrete taxa in asexual populations, but there is a limit to the degree of diversification that can evolve in a single population, determined by the expected *Tmrca*. Therefore, a more interesting comparison is the extent to which asexuals and sexuals diversify beyond levels expected in these simple null models. Two conditions cause diversification at this level: diversifying selection and geographic isolation.

DIVERSIFYING SELECTION IN A SINGLE POPULATION

Most models of sympatric speciation investigate how diversifying selection might cause a single sexual population to split into two reproductively isolated species. But how does the likelihood of sympatric divergence depend on the presence or absence of sex? Genealogical theory developed for frequency-dependent selection applies to this scenario. If two or more variants at a single locus experience frequency-dependent selection, then providing mutational shifts between them are relatively rare, the expected gene tree is shown in Figure 2E (Hudson 1991). We expect to observe two clades in the tree, corresponding to the two variants maintained by selection. The *Tmrca* is greater than in the neutral case. In asexual populations, frequency dependent selection at a single locus with rare mutation would lead to the formation of two clusters recognizable across the whole

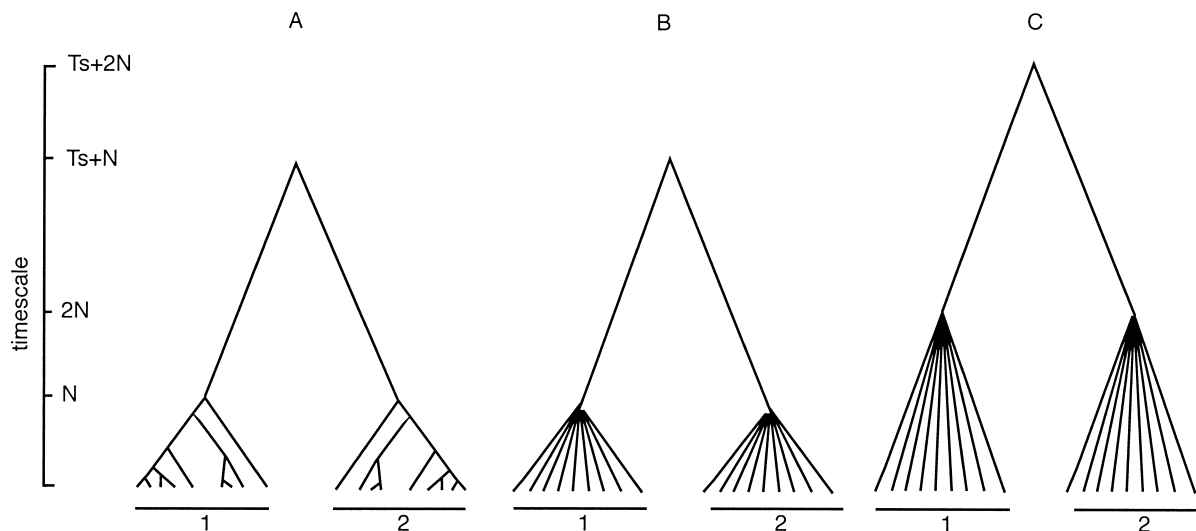


FIG. 3. Consensus gene trees from multiple loci sampled across two populations geographically isolated at time T_s , each with population size $N/2$. (A) Asexual haploid population. Assuming neutral coalescent, the T_{mrca} within each population is N generations. (B) Sexual haploid population. Same as (A) except for lack of resolution in consensus trees. (C) Sexual diploid population. Assuming neutral coalescent, the T_{mrca} within each population is $2N$ generations. Note we assume that $T_s \gg 2N$; that is, that coalescence within populations is complete at time of sample.

genome. In sexuals, frequency dependent selection at a single locus will only produce clustering at linked loci.

If diversifying selection acted on multiple gene traits, for example, caused by the existence of two habitat types, then divergence in the asexual population could proceed by stepwise accumulation of successive beneficial changes in each cluster. In contrast, adaptive divergence could only occur in the sexual population if assortative mating evolved concurrently (Felsenstein 1981; Dieckmann and Doebeli 1999). If assortative mating did arise, for example, mediated by local mating or pleiotropic effects of adaptive change (Rice 1987), then divergence might proceed faster in sexuals than asexuals because sweeps can occur simultaneously at multiple loci. However, sympatric adaptive divergence in sexuals, although possible, is widely believed to be less frequent than allopatric divergence because of the need for assortative mating (Turelli et al. 2001). To the extent that this belief is true, sympatric divergence will be easier in asexuals, which have no such requirement.

GENE TREES FOLLOWING GEOGRAPHIC ISOLATION

Barrier to Gene Flow in the Neutral Case

We consider an ancestral population of size N that at time T_s splits into two populations of size $N/2$ with no gene flow. For simplicity, we consider an equal split, but our conclusions do not depend on this assumption. In asexuals, the barrier to migration means that after roughly N generations from the onset of isolation, each population coalesces to a single ancestor (because the population sizes are $N/2$). Therefore, we expect two discrete genotypic clusters, with the age of the split between them equal to $T_s + N$, in which N is the expected T_{mrca} for two alleles chosen at random from the ancestral population at the time of split (Fig. 3A; Edwards and Beerli 2000).

In haploid sexuals, we expect a similar pattern because the

neutral coalescent is the same. The only difference is that each asexual population would display hierarchical variation of multilocus genotypes or traits, whereas the sexual populations would not (Fig. 3B). Therefore, the rate and extent to which sexuals and asexuals form discrete clusters in geographic isolation is the same, all other things being equal. If the sexuals were diploid, the T_{mrca} within each cluster would be twice that in the asexual case. This would increase the size of each cluster in genotypic space relative to the gap between them (Fig. 3C).

The important feature of this scenario is that a single limited population is split into two populations of smaller size, whose population sizes are limited independently of each other. After the split, the probability that an individual contributes to future generations depends only on the number of individuals in the same population, and hence the populations evolve independently. Constant population size is not necessary for these predictions, just some form of limitation on population growth. Similarly, assuming that sexuals and asexuals are equally likely to form splits of a particular size, allowing unequal splits of the ancestral population would not affect the qualitative predictions.

Barrier to Gene Flow with Selection

Divergent selection between the two populations, for example, due to environmental differences between areas, can speed up the formation of clusters (Cohan 1998). In asexuals, the entire genome will be homogenized by the most recent selective sweep, and therefore we might observe stronger clustering across multiple loci than in sexuals, depending on what proportion of the sexual genome experiences hitchhiking. However, if sexuals adapt faster to their environment than asexuals, the rate and magnitude of adaptive divergence between the two populations might be greater in the sexual case. Although discrete clusters in adaptive traits, such as

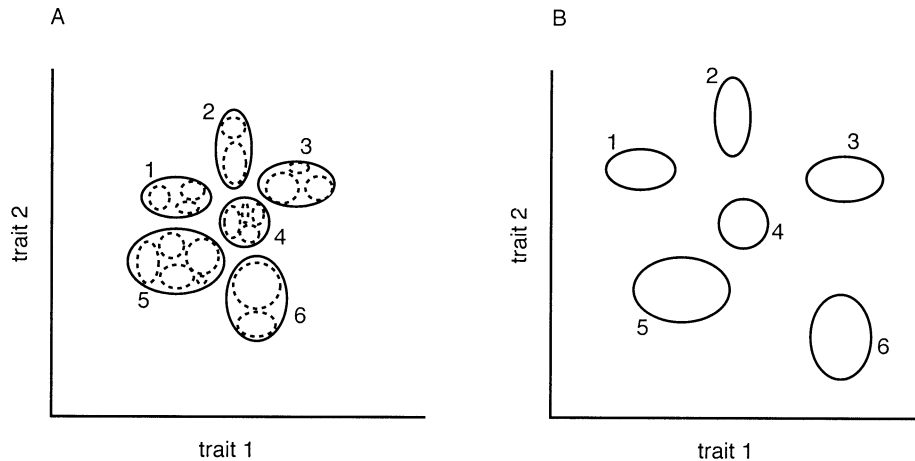


FIG. 4. Expected variation among clusters for two adaptive characters coded by multiple loci in (A) asexual and (B) sexual cases. Each ellipse represents the range of values observed within a single recognizable cluster. Note that the asexuals display further discreteness within each major cluster, due to the inherent tree structure of quantitative variation in asexual populations. The traits could be morphological measures or the first two principal components from a principal components analysis of a set of morphological characters. The number of clusters is the same in the sexual and asexual case, but the magnitude of differences among clusters (disparity) is greater in sexuals.

functional morphology, are expected in asexuals, they might be based on a smaller number of characters or smaller quantitative differences than in sexuals (Fig. 4). The same logic applies to divergence by differential responses to uniform selection.

Other types of selection will have less effect on the relative strength of cluster formation in sexuals and asexuals. For example, background selection against deleterious alleles might reduce *Tmrca* in asexuals slightly compared to sexuals (because of complete linkage), principally at intermediate selection coefficients (Neuhauser and Krone 1997). Similarly, diversifying selection in the ancestral population that remained in each daughter population could create a complicated pattern of coalescence and clustering, but the relative performance of sexuals and asexuals is a direct combination of scenarios discussed already.

Re-establishment of Sympatry

Suppose the barrier to migration is removed. There is now a population of N individuals, $N/2$ of which come from each population. In the asexual case, assuming that all individuals have an equal chance of contributing to the next generation, the expected gene tree will return gradually to a single coalescent with common ancestor at $2N$ generations (assuming neutral coalescence). There will be an equal chance that the common ancestor came from either population 1 or 2. If the two populations remain independently limited, that is adapted to different niches, the clusters will be stable in the face of population mixing (Cohan 2001).

In the sexual case, with or without interbreeding, the combined population will also return to a single coalescent with common ancestor $2N$ generations ago unless the two populations are independently limited. With interbreeding, the genome-wide pattern of clustering will be lost within a few generations, but each locus will retain the signature of two clusters for up to roughly $2N$ generations (Avise 2000). Unlinked loci could have ancestral genes from different popu-

lations. With no interbreeding, the ancestral gene at all loci will come from the same population (as in the asexual case). This scenario is similar to competitive extinction of one population by the other, but it occurs with no difference in competitive ability between them, simply by the chance contributions of individuals to future generations.

Therefore, for sexuals and asexuals, independent limitation of population size is a key requirement for the stable coexistence of discrete clusters. This requires ecological differences between the two populations, that is that they are limited by different factors in their shared environment. Without such differences, any clusters formed in isolation will eventually collapse back to a single cluster. The only alternative would be that rates of cluster formation were fast enough for clusters to exist at a steady state between formation and extinction without the need for stable coexistence (Hubbell 2001).

The significance of sexual reproduction for coexistence is twofold. First, if individuals from the two populations interbreed when isolation is removed, differences based on multiple incompletely linked loci will be eroded quickly (Felsenstein 1981). Hence, if the rate of evolution of reproductive isolation is limiting, sex will counteract the tendency for clusters to persist in sympatry. Second, by speeding up adaptive divergence between isolated populations, sexual reproduction might increase the chance that enough adaptive differences exist between the two populations for them to coexist. The net outcome will depend on the balance among rates at each step of cluster formation. For example, if environmental events causing isolation and secondary contact are rare, there might be time for both sexuals and asexuals to evolve into discrete clusters with sufficient divergence to persist even if contact is re-established. Instead, if environmental events are frequent, stable clusters might only have time to form in sexual lineages, and then only if reproductive isolation keeps step with rates of adaptive divergence.

DISCUSSION

We conclude that asexual organisms are expected to diversify into discrete genetic and morphological clusters similar to those found in sexual organisms, as a result of divergent selection and/or geographic isolation. In both sexuals and asexuals, stability of clusters in sympatry requires independent limitation of population size, implying different niches, otherwise one cluster will be lost within a few N generations. This is a simple consequence of standard population models, and does not rely on special assumptions about ecology or competition. In sexuals, reproductive isolation is also necessary otherwise genetic differences between clusters will be lost in just a few generations. Whether asexuals or sexuals are likely to display more clusters following a given series of events will depend on the balance among different stages of cluster formation.

We have intentionally avoided using the term “species” because of the difficulty of applying a universal species concept. Instead, we focused on the formation of genotypic and phenotypic clusters. Although such clusters are a part or consequence of most species definitions, we emphasize that defining species is not necessary for our argument. We believe our conclusions offer general insights into diversification, irrespective of exact species concept subscribed to.

Our account makes several simplifying assumptions. We assumed extreme cases, but of course there can be intermediates, such as partial recombination, partial gene flow, etc. An explicit model of diversification could be devised to look at these complexities and the interactions among different stages. In particular, the frequency of environmental events causing changes in population structure or selection regime is an important parameter. Details of the external world are often left out of population genetic models or treated as given, but these details can have a major effect on outcomes.

Also, we assumed that recombination is the only difference between sexuals and asexuals, but in real comparisons this is unlikely to be true. For example, asexuals may be more prone to gene duplication or rearrangements, because there is no constraint for genomes to align at meiosis (Blackman et al. 2000). If these changes play a role in adaptive evolution (Lynch and Conery 2001), this could affect relative rates of adaptive change in sexuals and asexuals.

Another difference is that sexuals and asexuals might occupy different habitats. For example, bdelloid rotifers tend to be found in unpredictable, desiccating habitats and have dispersive, drought-resistant stages (Ricci 1987). Asexuality is one of a suite of characters that allow bdelloids to thrive in these habitats, permitting fast reproduction without the need for a mate. In contrast, sexual monogononts occupy habitats with more predictable water-availability and survive drought in the form of resting eggs. Differences in dispersal rates could affect the tendency to form clusters by geographic isolation, and also how organisms experience spatial environmental variation. Interestingly, most ancient asexuals are in the 1-mm size range often linked to global dispersal capabilities (Finlay and Clarke 1999; but see Walter and Lindquist 1995; Schon et al. 1998).

So how do our predictions compare to patterns in the real

world? The most striking feature of asexuality is that strictly asexual lineages are relatively scarce and tend to be of recent origin (Bell 1982; Judson and Normark 1996). For example, most asexual plant species result from recent, highly polyphyletic origins of asexuality (Mogie 1992). The resulting diversity can probably be explained mainly by diversification in sexual progenitors, rather than by strictly asexual diversification. However, some origins of asexuality might have undergone subsequent diversification, for example, *Taraxacum* section *hamata* comprises a well-established monophyletic group of 25 named apomictic species (Kirschner and Stepanek 1996). Whether these taxa represent diversification beyond levels that are expected in a single asexual population is unclear. Other examples appear to conform well to expected patterns in a single asexual population, for example, the taxonomic continuum of clones found in the genus *Alchemilla* (Maynard Smith and Szathmary 1995; Sepp and Paal 1998).

The lack of diversity in asexual clades could be interpreted as evidence for a reduced tendency to form clusters in asexuals, that is lower origination rates. However, the alternative is that asexuals have higher extinction rates than sexuals because of their failure to keep pace with changing biotic and abiotic environments and mutational loads (Burt 2000). In this case, many asexual lineages might simply not last long enough for clusters to form, even though their rates of cluster formation could be the same as or greater than that of sexuals.

Fortunately, a few long-lived asexual clades are known that can be compared to sexual relatives. The largest is the bdelloid rotifers, comprising around 360 named species. Recent genetic tests support their asexual status, finding no evidence for cryptic sex (Mark Welch and Meselson 2000). Bdelloid species have been consistently recognized by taxonomists (Holman 1987), and preliminary mtDNA data support the existence of genetic clusters in the group (C. W. Birky, unpubl. data). However, morphological differences between bdelloid species can be slight, and gross morphology is more uniform in bdelloids than in their closest sexual relatives, the monogonont rotifers (Ricci 1987). Monogononts also comprise more species and occupy a broader range of trophic niches (Donner 1966; Wallace and Snell 1991). These differences might reflect lower rates of adaptive evolution in bdelloids, or a more recent origin for bdelloids. Phylogenetic tests are needed to test these alternatives.

Other clades of putative ancient asexuals with apparent diversity exist (Judson and Normark 1996; Schon et al. 1998; Burt 2000), particularly in protists, fungi, and mites, some with genetic evidence for prolonged asexuality (Kuhn et al. 2001). These examples are suggestive of diversification in long-lived asexual lineages, and more speculatively of low rates of adaptive divergence, but at present the evidence is largely anecdotal. Quantitative comparisons of adaptive divergence and degree of clustering in related sexual and asexual clades are desperately needed, together with genetic tests to confirm the sexual or asexual history of the clades. Current phylogenetic and genealogical methods, combined with functional morphometrics, provide the tools for these studies (Avisé 2000; Monteiro et al. 2000; Barraclough and Nee 2001). Studies are needed on both recent and ancient asexual groups,

to obtain a comprehensive view of the effects of sexuality on diversification.

Returning to the questions raised in the introduction, we conclude that sexual reproduction is not a necessary condition for diversification into discrete genetic and morphological entities. Asexuals are not expected to display a continuum of forms, not only because of their tree-like ancestry, but also because the processes causing diversification in sexuals are expected to have similar effects in asexuals. In at least some cases, these processes will be more effective in asexuals than in sexuals, but whether sexuals or asexuals display stronger overall patterns of diversification is an empirical question. Irrespective of sexuality, diversification is an inevitable consequence of the complexity of the physical world, either through isolation in different geographic areas or adaptive divergence in a heterogeneous environment. But comparisons between sexuals and asexuals could shed light on the importance of adaptive evolution for the origin and persistence of diversity. Confounding factors aside, the only explanation we can see for stronger patterns in sexuals rather than asexuals is if faster rates of adaptive change promote greater clustering.

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