SHORT COMMUNICATION

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Niche differentiation among clones in asexual grass thrips

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Abstract

Many asexual animal populations comprise a mixture of genetically different line-
ages, but to what degree this genetic diversity leads to ecological differences remains
often unknown. Here, we test whether genetically different clonal lineages of
Aptinothrips grass thrips differ in performance on a range of plants used as hosts in
natural populations. We find a clear clone-by-plant species interactive effect on re-
productive output, meaning that clonal lineages perform differently on different
plant species and thus are characterized by disparate ecological niches. This implies
that local clonal diversities can be driven and maintained by frequency-dependent
selection and that resource heterogeneity can generate diverse clone assemblies.

KEYWORDS

clonal diversity, frozen niche variation, general-purpose genotype, parthenogenesis, Poaceae,
reproduction

1 | INTRODUCTION

The continuous generation of genetic variation for fitness is re-
garded as one of the main explanations for the predominance of
sex in eukaryotes (Bell, 1982). Theoretical studies have shown that
under some conditions, sex can be favoured over asexuality because
it creates novel and/or rare genotypes (Bell, 1982; Otto, 2009). Such
novel and rare genotypes are favoured under negative frequency-
dependent selection or in habitats with spatially heterogeneous
or temporally fluctuating resources. For example, one component
of the "parasite hypothesis for sex" implies negative frequency-
dependent selection, as it predicts that parasites evolve to track
common host genotypes (Dagan, Liljeroos, Jokela, & Ben-Ami, 2013;
Decaestecker et al., 2007; Morran, Schmidt, Gelarden, Parrish, &
Lively, 2011). Similar ideas are available for selection imposed by re-
sources; that is rare genotypes are able to exploit resources where
competition is low (reviewed by Scheu & Drossel, 2007).

Theories for the maintenance of sex generally assume genet-
ically uniform populations of asexuals, whereas in nature, many
asexual animal and plant populations comprise genetically distinct

clones (Bell, 1982; Ellstrand & Roose, 1987; Jokela, Dybdahl, &
Lively, 1999; Parker, 1979). Indeed, high genetic diversity is the case
in many asexual populations (Fontcuberta García-Cuenca, Dumas, &
Schwander, 2016; Kearney et al., 2009; Moritz, Donnellan, Adams,
& Baverstock, 1989; Neiman, Jokela, & Lively, 2005; Pannebakker,
Zwaan, Beukeboom, & Van Alphen, 2004; Tully & Ferrière, 2008;
Vorburger, Lancaster, & Sunnucks, 2003), but whether clonal diver-
sity is generally associated with phenotypic and ecological diversity
remains unknown. Genetic diversity in asexuals can be due to lineage
diversification after the transition to asexuality (owing to mutation
accumulation) and because asexuals have different sexual ancestors;
that is they arose via independent transitions to asexuality (Janko,
Drozd, Flegr, & Pannell, 2008). Such independent transitions are
especially likely to generate ecological differentiation (Bell, 1982;
Janko et al., 2008; King, Jokela, & Lively, 2011). More generally, it
will be difficult to explain the maintenance of sex via its effect on
genetic diversity if sexual species compete with genetically diverse
rather than genetically uniform asexuals (Judson, 1997).

In this study, we test whether genetic differentiation in asex-
ual *Aptinothrips* (Thysanoptera: Thripidae) grass thrips is neutral or
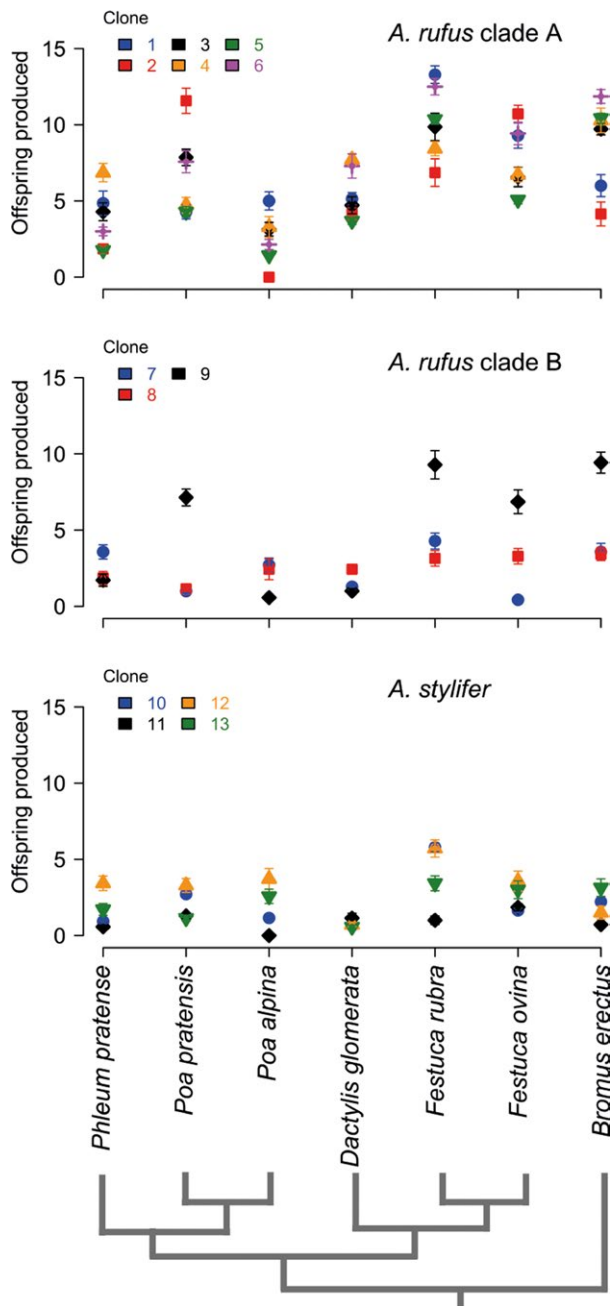
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FIGURE 1 Number of offspring produced by different asexual *Aptinothrips* lineages on seven host plant species. Every panel depicts the asexual lineages of an independently evolved asexual clade (identified in van der Kooi and Schwander (2014)). For every lineage, the mean ± 95% confidence interval (assuming a normal distribution) is shown

ecologically relevant. *Aptinothrips* is a system where asexuality has evolved several times independently and is associated with a large geographic distribution and extreme genetic diversity (van der Kooi & Schwander, 2014). We test whether thirteen genetically different clonal lineages of *Aptinothrips rufus* and *Aptinothrips stylifer* occupy different ecological niches by examining their performance on seven common host plant species. In a breeding experiment and using the number of offspring produced as a proxy for fitness, we show that different clonal lineages indeed feature different ecological niches.

2 | MATERIALS AND METHODS

2.1 | Study species and breeding

Aptinothrips grass thrips are small (1–2 mm), wingless insects that feed on various species of Poaceae. For *A. rufus*, asexuality evolved at least twice independently (van der Kooi & Schwander, 2014) as inferred from phylogenies based on mitochondrial sequences. Asexual populations of this species can be found all over the world and exhibit very high levels of mitochondrial diversity, whereas sexual populations only occur in the Mediterranean region and exhibit a relatively low mitochondrial diversity (Fontcuberta García-Cuenca et al., 2016; van der Kooi & Schwander, 2014). The species *A. stylifer* evolved asexuality independently from *A. rufus* (van der Kooi & Schwander, 2014), and different populations also comprise a pool of genetically different individuals (see Results). Nine and four genetically different females of *A. rufus* and *A. stylifer* were isolated from three locations in Switzerland (Supporting Information). These individuals were used to establish thirteen iso-female lines (hereafter: clonal lineages); for each lineage, third-generation individuals were used in the experiment.

2.2 | Experimental design

We tested the performance of asexual females on seven grass species that are commonly found in natural habitats: meadow brome (*Bromus erectus*), alpine bluegrass (*Poa alpina*), common meadow-grass (*Poa pratensis*), red fescue (*Festuca rubra*), sheep fescue (*Festuca ovina*), Timothy grass (*Phleum pratense*) and orchard grass (*Dactylis glomerata*). For each clonal lineage, 7–14 replicate individuals were tested on each host plant species; this yielded a total of 735 replicates (see Supporting Information). The experiment was performed in July–August 2016; for logistic reasons, it was performed in two batches separated by 4 days.

2.3 | Data analysis

To test for ecological variation among species and clonal lineages of *Aptinothrips*, we used linear mixed models (LMMs) as implemented in the R package *lme4* (Bates, Maechler, Bolker, & Walker, 2014) in R 3.4.2. We tested whether thrips species, independent transitions to asexuality within *A. rufus*, clonal lineage, the grass species and their interactions affected the number of offspring. Batch was included as a random factor in the model. Significance was tested using a permutation ANOVA (Supporting Information).

3 | RESULTS

We observed clear differences in the number of offspring produced by asexual *Aptinothrips* (Figure 1). There was an effect of thrips species ($df = 1$, $p < 0.01$) and an effect of clade, that is, independent transitions to asexuality ($df = 2$, $p < 0.01$), on the number of offspring produced. In line with our hypothesis of ecological divergence,

TABLE 1 Overview of species that show ecological diversification of clonal lineages

Asexual species investigated	Common name	Approach	Results	Reference
Erigeron annuus	Eastern daisy fleabane	Experimentally test the number and size of seeds, biomass allocation and seed germination for different lineages.	Variation in seed size, allocation to roots and seed germination for different lineages.	Stratton (1991)
Taraxacum officinale	Dandelion	Experimentally test the effect of drought and shade on biomass allocation for different lineages.	Lineages often perform differently under different conditions.	Oplaat and Verhoeven (2015)
Rhopalosiphum padi	Cherry oat aphid	Experimentally test fecundity and longevity of clones on different plant species at two temperatures.	Small differences between lineages; performance in laboratory experiment is correlated with abundance in natural populations.	Valenzuela, Ridland, Weeks, and Hoffmann (2010)
Myzus persicae	Peach potato aphid	Experimentally test reproductive success of lineages on different host plant species.	Lineages perform differently on different host plant species.	Vorburger, Sunnucks, and Ward (2003)
Folsomia candida	Springtail	Experimentally test reproductive investment and survival for different lineages.	Significant variation between lineages in number and size of offspring produced.	Tully and Ferrière (2008)
Daphnia pulex	Water flea	Experimentally test lineage performance in different locations with different salinities.	Lineages perform differently in different regions, consistent with local adaptation.	Weider and Hebert (1987)
Potamopyrgus antipodarum	Fresh water snail	Field sampling in different populations.	In different populations, different lineages feature specific dietary preferences.	Jokela et al. (1999)
Heterontia binoei	Gecko	Field sampling of lineages in natural populations with different climates.	Lineages with different origins occupied different geographic regions and niches.	Kearney, Moussalli, Strasburg, Lindenmayer, and Moritz (2003)
Lepidodactylus lugubris	Gecko	Field sampling of lineages in natural habitats.	Two common lineages feature different niches, though with some overlap.	Hanley, Bolger, and Case (1994)
Aptinothrips rufus & A. stylifer	Grass thrips	Experimentally test performance of different lineages on seven common host plant species.	Lineages perform differently on different host plant species	This study

different clonal lineages are characterized by different ecologies, as revealed by significant clone-by-plant species interaction effects on clonal lineage performances (df = 72, p < 0.01). Ecological differences among clonal lineages are not solely explained by independent transitions to asexuality as clonal lineages within one *A. rufus* clade (clade B in Figure 1) also differ from each other (df = 12, p = 0.04); the small sample sizes in *A. stylifer* preclude performing a similar analysis.

4 | DISCUSSION

Many asexual populations comprise a large number of different clonal lineages (Bell, 1982; Parker, 1979), but whether genetically different clones feature different ecologies is largely unknown. In this study, we showed that different clonal *Aptinothrips* lineages feature different ecological niches (Figure 1). Ecological divergence of clonal lineages is pronounced both within and between independently derived asexual clades. Although assessing the relative importance of independent transitions versus within clade divergence requires deeper sampling, the multiple origins of asexuality in *Aptinothrips* (van der Kooi & Schwander, 2014) have increased the genetic diversity in asexuals and likely contribute to their extreme ecological success.

The facts that asexual *Aptinothrips* populations exhibit a higher genetic diversity than sexuals (Fontcuberta García-Cuenca et al., 2016; van der Kooi & Schwander, 2014) and that this genetic diversity translates to ecological divergence (this study) may explain why asexuals outcompete sexuals in mesocosm experiments (Lavanchy et al., 2016). Our findings further suggest that locations with different grass species would select for different sets of clonal lineages. High grass species diversity is expected to promote and maintain clonal diversity in the thrips population, because more grass species reflect more niches available for different clonal lineages. An interesting open question is whether temporal fluctuations in plant species frequency lead to fluctuating clone frequencies, as was previously found in the aphid *Myzus persicae* by Vorburger (2006).

A review of literature showed that clonal diversity is associated with ecological diversity in a suite of at least nine additional plant and animal species (Table 1). This includes aquatic and terrestrial asexual systems with very diverse ecologies. Taken together, these studies convincingly show that populations of clonal animals comprise ecologically relevant genetic variation and that clonal diversity should therefore not be disregarded in theory on the maintenance of sex in nature.

Asexuals are frequently more ecologically successful than related sexuals, which is often believed to be due to the reproductive assurance conferred by asexuality (e.g., Bell, 1982), but this may not be the sole explanation. For example, a recent large-scale comparative study showed that asexuals have 2–3.5 times as many host species and occur in up to five times as many countries compared to their sexual counterparts, highlighting the (ecological) success of asexuality (van der Kooi, Matthey-Doret, & Schwander, 2017). Our

current study shows that in addition to the reproductive advantage of asexuality, high genetic diversity can contribute to the success of asexuals.

To summarize, genetic diversity in asexual *Aptinothrips* lineages is associated with ecological diversity. Under such ecological differentiation of clonal lineages, which appears to occur in a suite of asexual animal and plant systems (Table 1), natural selection may maintain clonal diversity rather than sex. Future theory on the maintenance of sex would benefit from incorporating clonal diversity, different clonal diversity-generating mechanisms and their ecological significance.

CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

CJvdK, KG and TS designed the study. CJvdK, DA and KG carried out the experiment and analysed the data. CJvdK and KG wrote the first draft of the manuscript. All authors edited the manuscript and approved the final version.

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SUPPORTING INFORMATION

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