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242

Veronica Chevasco

Evolution and Ecological Aspects of Parthenogenetic and Sexual Bagworm Moths (Lepidoptera: Psychidae: Naryciinae)

JYVÄSKYLÄN YLIOPISTO

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UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2012

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To my parents, Carlos and Elsa

ABSTRACT

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Evolution and ecological aspects of parthenogenetic and sexual bagworm moths (Lepidoptera: Psychidae: Naryciinae)
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The prevalence of sex could be explained by the benefits of recombination. Due to the inherent advantages of sex, parthenogens are considered as an evolutionary dead–end. However, the apparent success of some parthenogenetic species constitutes one of the most intriguing questions in evolutionary biology and deserves investigation. In this dissertation I investigated the origin of parthenogenesis and examined factors contributing to its maintenance in bagworm moths. A DNA barcoding approach was conducted as an accurate way to identify species. The identification of sexual species was vital to test the hypothesis of a possible hybrid origin leading to allopolyploidy in parthenogenetic species. Nonetheless, the phylogenetic results rejected the possibility of hybridization. An alternative scenario for the origin of parthenogenetic *D. fennicella* is the possibility of autopolyploidization of a closely related sexual species, such as *D. lazuri*. Parthenogenesis may be favored if the sexual wingless females face a high risk of remaining unfertilized. The results showed that male sperm limitation may not have a significant role as a selective force to promote the spread of parthenogenesis, because females tend to re–mate if the first mating fails. Continuing to investigate potential reasons for the success of parthenogenetic species, *D. fennicella* was found to be less vulnerable to parasitoid attacks than sexual species, which contradicted one prediction of the parasite hypothesis of sex. Parthenogens could be avoiding parasitoid attacks due to differences in phenology between sexual and parthenogenetic species. An alternative explanation might be the unexpected genetic variability that was found in parthenogenetic *D. fennicella*. In conclusion, a plausible explanation for the occurrence of the parthenogenetic *D. fennicella* could be that its polyploid status might provide enough advantages to overcome a higher mutational load, lower genotypic variation, and parasitoid attacks in the absence of sexual reproduction.

Keywords: Barcoding, genetic diversity, parthenogenesis, polyploidy, sex.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I–V.

I Chevasco, V., Elzinga, J.A., Mappes, J., Grapputo, A. 2012. Evaluating criteria for species identification in bagworm moths (Lepidoptera: Psychidae). Manuscript.

II Chevasco, V., Elzinga, J.A., Galarza, J.A., Mappes, J., Grapputo, A. 2012. Investigating the origin of parthenogenesis and ploidy level in *Dahlica fennicella* (Lepidoptera: Psychidae). Manuscript.

III Elzinga, J.A., Chevasco, V., Grapputo, A., Mappes, J. 2011. Influence of male mating history on female reproductive success among monandrous Naryciinae (Lepidoptera: Psychidae). *Ecological Entomology* 36: 170–180.

IV Elzinga, J.A., Chevasco, V., Mappes, J., Grapputo, A. 2012. Low parasitism rates in parthenogenetic bagworm moths do not support the parasitoid hypothesis for sex. Submitted manuscript.

V Chevasco, V., Elzinga, J.A., Viinikainen, S.M., Mappes, J., Galarza, J.A. 2012. Unexpected genetic variability in the parthenogenetic bagworm moth *Dahlica fennicella* (Lepidoptera: Psychidae) revealed by novel microsatellite markers. *Conservation Genetics Resources*. 4: 159–162.

The table shows the contributions to the original papers.

	I	II	III	IV	V
Original Idea	AG, VC, JAE, JM	VC, AG, JAE, JM	JAE, JM	JAE, JM, VC, AG	JAG, VC
Data	VC, SV, JAE	VC, SV, JAE	JAE, VC, SV	JAE, SV, VC	SV, VC, JAG
Analyses	VC, AG, JAE	VC,AG, JAE	JAE	JAE	VC, JAG, JAE
Writing	VC, JAE, AG, JM	VC, JAE, JAG, JM, AG	JAE, JM, AG, VC	JAE, JM, AG, VC	VC, JG, JAE, JM

VC = Veronica Chevasco, AG = Alessandro Grapputo,
JM = Johanna Mappes, JAE = Jelmer Elzinga, JAG = Juan Galarza,
SV = Sari Viinikainen.

1 INTRODUCTION

1.1 The widespread occurrence of sex

The prevalence of sexual reproduction among eukaryotes has generated a high degree of interest and is often called the "queen of problems in evolutionary biology" (Bell 1982). Plausible explanations to explain the dominance of sexual reproduction have been proposed since Darwin. As early as 1837, Darwin proposed that sex was advantageous because of variation and the unification of species. Nevertheless, later on he suggested that sex exists to generate vigorous offspring (Darwin 1859). The idea of variation and the origin of new chromosomal combinations was not suggested until 1893 by Weismann.

Currently, the most widely accepted hypothesis for the prevalence of sexual reproduction is that sex generates genetic variability through recombination, which allows an adaptive response to environmental changes (Fisher 1958, Burt 2000). Recombination also eliminates deleterious mutations (Muller 1964, Kondrashov 1988, Birky 1999, Rice & Friberg 2009) and fixes rare beneficial modifications (Kondrashov & Kondrashov 2001). Additionally, sex is considered a repair mechanism for double–strand breaks in DNA (Bernstein 1998) and a tool to restore DNA methylation (Holliday 1988). Other theories (Bell 1982), Kondrashov 1993, Barton & Charlesworth 1998) state that natural selection works better with sexual reproduction because recombination breaks up negative gene combinations. Sex also produces genetically diverse offspring that can exploit a broad range of resources, as stated by the Tangled Bank hypothesis (Maynard Smith 1978, Bell 1982). Additionally, genetically diverse offspring can dominate in complex environments (Song et al. 2012). While many theories consider sexual reproduction as beneficial, Margulis & Sagan (1986) do not consider sexual reproduction to be advantageous *per se* but simply as an inherited feature from eukaryotic ancestry.

One of the most widely accepted hypotheses to explain the maintenance of sex and recombination is a specific case of the Red Queen hypothesis (RQH) known as the parasite hypothesis of sex (Van Valen 1973). It states that asexuals

are more susceptible to parasitoid attacks due to their limited ability to generate new genotypes because they lack recombination. According to (Lively 2010), parasitoids are under selection to infect the most common genotypes. Consequently, if an asexual clone is the most common genotype in mixed populations the parasites would be expected to evolve to infect the most common clone. However, the main assumption of the parasite hypothesis of sex is only applicable if: (a) the sexual and asexual species have similar ecological and behavioural traits, (b) sexuals are more genetically diverse than the asexuals and (c) within–species individual diversity is similar in sexuals and asexuals (Tobler & Schlupp 2010).

Regardless of the wide range of theories, conclusive evidence for the predominance of sex is still unresolved. For instance, a definitive verdict for the application of the RQH for the predominance of sexual reproduction requires more empirical (Peters & Lively 2007) and theoretical work (Gandon & Otto 2007).

1.2 The costs of sex

Despite many advantages, sex involves several costs. Based on its apparent costs, the occurrence of sex is a paradox. It is interesting to consider why asexuality has a low occurrence 0.1% (Suomalainen et al. 1987) since no apparent costs are involved. There are two costs traditionally attributed to sexual reproduction. Firstly, asexual females avoid the "two–fold cost of sex" as they have twice the reproductive rate if compared with sexuals because males can not give birth to any offspring (Maynard Smith 1978). Second, the cost of sex is also attributed to genome dilution because only half of the parental genome is transmitted to the offspring (Williams 1975). Nevertheless, the cost of sex is context dependent (Lehtonen et al. 2011). For instance, the cost of males is rarely two fold since twofoldness assumes that males do not assist or hinder females in offspring production. Additionally, only genes that determine the mode of reproduction are important, and the dilution of other genes is irrelevant.

Some other costs involve the localization of potential mates, an elaborate courtship/mating behaviour, courtship and competition with rival suitors. These costs fall mainly upon males while females might share the costs in a lesser extent (Daly 1978). Nevertheless, females might face the risk of injury when aggressive courtship elements are involved (Daly 1978). Furthermore, the transfer of seminal toxins and the evolution of genital barbs and spines serve as means by which males can induce females to delay or avoid remating (Johnstone & Keller 2000). Additional costs include exposure to predators while mating, and the spread of disease (Crow 1999).

In summary, the paradoxical dominance of sex is not well understood. Therefore, in order to gain more insights into its prevalence, the study of asexuality might contribute to solve its extensive incidence.

1.3 Is asexuality an evolutionary dead–end?

In spite of its overwhelming costs, a sexual reproductive strategy confers a wide range of benefits. Considering the advantages of sex, an asexual reproductive strategy might seem disadvantageous since asexual species are subjected to the accumulation of deleterious mutations or Muller´s ratchet (Muller 1964) and are more susceptible to parasite attacks (Van Valen 1973). Moreover, asexuals would not be able to fix advantageous mutations to adapt to different habitats, producing a high rate of extinction and a low rate of speciation (Birky et al. 2005). As a result, asexual lineages could be considered an evolutionary dead end based on a traditional point of view (White 1973, Bell 1982). Alternatively, Silvertown (2008) suggested that the existence of asexual reproduction is linked to the failure of sex, prolonging the time to extinction.

In spite of the generalized idea that considers parthenogenesis as a dead–end, there are several aspects that need to be considered. First of all, the reproduction of parthenogenetic species is not constrained by cytoplasmic, chromosomal or genomic incompatibilities between two individuals (Hörandl 2009). Another advantage is that in low density populations an asexual female does not face the risk of remaining unmated (Schwander et al. 2010, Rhainds 2010). In many species, this risk can be considerable high, underlying serious evolutionary consequences (Kokko & Mappes 2005).

Parthenogenesis is often thought to automatically preclude organisms from being genetically variable, but this is not the case. Therefore, it is a misconception to think that parthenogens and other asexual organisms completely lack variation at the genetic level. Although some parthenogens can produce virtually identical offspring (via apomictic parthenogenesis) as in rotifers (Simon et al. 2003), some inherent cytological mechanisms (automictic parthenogenesis) can even maintain meiosis as in the parthenogenetic bagworm moth *Dahlica triquetrella* (Stenberg & Saura 2009) and produce variable offspring as in stick insects (Scali 2009) and parasitoids (Beukeboom & Pijnacker 2000) (Fig. 1).

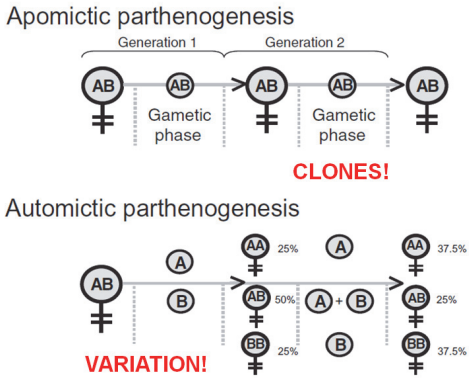

FIGURE 1 Parthenogenetic modes of reproduction (modified from Simon et al. 2003).

Given some genetic variation, reproducing without the genetic contribution of male gametes might partly explain the apparent success of some parthenogenetic species that proliferate nowadays, such as bdelloid rotifers (Mark Welch & Meselson 1998) aphids (Blackman et al. 2000) and stick insects (Schwander & Crespi 2009). Moreover, the existence of ancient parthenogens such as the ostracods *Vestalenula matildae* and *V. marmonieri* (Schön et al. 2010), the mite *Archegozetes longisetosus* (Heethoff et al. 2009) and bdelloid rotifers (Mark Welch & Meselson 2000) supports the idea that sexual reproduction might not be essential for the abundance of certain species.

Other than a variety of cytological mechanisms, the proliferation of parthenogens could also be explained by two hypotheses for the evolution of niche breath: the "general purpose genotype" (GPG) (Vandel 1928) and the "frozen niche–variation" (FNV) models (Vrijenhoek 1979, Vrijenhoek 1984). The GPG model suggests that clones show broader tolerance to a variety of environmental conditions, making them able to exploit more niches compared to sexual species (Van Doninck et al. 2002, Vorburger et al. 2003). In contrast, the FNV model proposes that efficient specialist clones coexisting with a sexual ancestor could exclude sexuals (Harshman & Futuyma 1985, Tagg et al. 2005). Eventually, the clones from a parthenogenetic female could replace a sexual population (Lively 1996). However, this condition will be reached if "all else is equal" when comparing reproduction between parthenogenetic species and sexuals (Jokela et al. 1997).

According to all reported evidence, parthenogenetic species are characterized by alternative mechanisms that enable them to overcome all the possible disadvantages predicted by the traditional theories for the absence of sex.

1.4 Origin of asexual reproduction

Even though sex is considered as essential for the long persistence of a lineage, asexual reproduction is common among protists, plants, fungi and animals (Schurko et al. 2009). Among eukaryotes, sex appears to be ancestral (Malik et al. 2008). Therefore, all asexual lineages have sexual ancestors. The mechanisms by which asexuals originate is variable. In insects, a mutation could arise in genes that regulate sexual reproduction (Simon et al. 2003). A second possibility includes the transmission of asexual genes (i.e. by parthenogenetically produced males in *Daphnia pulex* (Innes & Hebert 1988). Other causes that induce parthenogenesis include bacterial infections such as *Wolbachia (*i.e. apomictic parthenogenesis in mites (Weeks et al. 2001) or *Cardinium (*i.e. parthenogenetic reproduction in the oleander scale (Provencher et al. 2005).

The most common route to asexuality is by hybridization, which has important implications as a main factor to increase adaptive potential (Hörandl 2009). Hybridization is often linked to the origin of apomictic plants (Grimanelli et al. 2001, Bicknell & Koltunow 2004, Carman 2007). In contrast, hybridization is usually rare among animals, especially when compared with plants (Hörandl

2009). Nevertheless, hybridization does occur in animals and it is mostly known from fish (Choleva et al. 2012) birds and butterflies (Mavárez & Linares 2008). Although hybridization might not be widespread in animals, the correlation between hybridization and parthenogenesis was considered to have two directions. According to Kearney et al. (2009) "there are two very different ways to view the link between hybridization and parthenogenesis, either parthenogenesis provides a mean to the end of an advantageous hybrid state, or the hybrid state itself provides a means to become parthenogenetic".

Hybridization between two different species or individuals from genetically distinct populations has profound effects in the ploidy levels of the descendants. Hybrid offspring is characterized by the occurrence of chromosome sets from both progenitors. For instance, if each of the parental species is diploid (2n) the resulting offspring will be tetraploid (4n). The occurrence of multiple sets of chromosomes as a result of interspecific hybridization is denominated allopolyploidy (Foighil & Smith 1995, Delmotte et al. 2003, Johnson 2006, Shinohara et al. 2010). Increased ploidy level can also be generated by autopolyploidization. Autopolyploidization results from a mutation in chromosome number (Comai 2005) or as a consequence of mitotic or meiotic failure of cell division (Otto & Whitton 2000). Alternatively, as suggested for the parthenogenetic tetraploid moth *Dahlica triquetrella* (Seiler 1961), autopolyploids can also be generated by the production of diploid unstable parthenogens followed by stabilized parthenogenesis (Stenberg & Saura 2009).

The multiple routes for the origin of parthenogenesis might constitute a feasible explanation for the occurrence of some species without the benefits of sex (Simon et al. 2003).

1.5 Polyploidy and parthenogenetic reproduction

Polyploidy and parthenogenetic reproductions are often found to be correlated (Suomalainen et al. 1987, Asker & Jerling 1992) mainly due to the advantages of duplicated genes. Polyploidy confers a wide range of benefits that might help parthenogens to cope with the lack of sex. Polyploidy is recognized as the primary cause of long term diversification, novelty and evolutionary success (Otto & Whitton 2000). Due to its multiple origins, which include allo and auto–polyploids (Mable 2004) polyploidy does not constitute a difficult evolutionary transition (Otto & Whitton 2000). Polyploid species are usually fit and well adapted, by being efficient competitors of their diploid relatives. Moreover, polyploids can be more vigorous than their diploid parents (heterosis) and they can mask the deleterious effects of mutations due to gene redundancy (Comai 2005).

Polyploid parthenogens show adaptations to extreme habitats and new environments. For instance, an example of geographic parthenogenesis includes the polyploid weevil *Otiorhynchus scaber*, which is a superior colonizer if compared to diploids (Stenberg & Lundmark 2004). Additionally, the higher ploidy

level in *Dahlica triquetrella* is linked to a wider distribution (Seiler 1961). Additionally, polyploids show greater levels of genetic variation than mutation and recombination alone may confer (Schurko et al. 2009). Due to the fact that polyploid parthenogens carry more alleles, each individual has a greater chance of having new beneficial mutations (Paquin & Adams 1983) and more opportunities to avoid parasites (Stenberg & Saura 2009). Lastly, parthenogens and the ones with apomictic parthenogenesis lack the obstacles of polyploidy, such as chromosomal sex determination (Stenberg & Saura 2009).

In spite of all the benefits of polyploidy, it has not always been considered as beneficial. White (1973) had a negative opinion about the evolutionary potential of polyploid parthenogens, and considered them as blind alleys of evolution due to their supposedly inability to respond to environmental changes. Some other negative views of polyploids includes the disrupting effects of cell and nuclear enlargement, production of aneuploid cells and epigenetic instability (Comai 2005).

In summary, the numerous benefits of polyploidy might counterbalance any possible disadvantages of multiple sets of chromosomes. Polyploidy might have long–term benefits by increasing rates of adaptive evolution for the apparent prevalence of certain parthenogens.

1.6 Aims

In this dissertation I investigated the origin of parthenogenesis and factors contributing to its maintenance in the bagworm moth *Dahlica fennicella* (Lepidoptera: Psychidae: Naryciinae). Bagworm moths constitute one of the few systems to study alternative reproductive strategies because parthenogenetic species appear to be as successful as the coexisting closely related sexual species.

Parthenogenetic reproduction is extremely rare in Lepidoptera (Rhainds et al. 2009). The parthenogenetic *D. fennicella* appears abundant in several populations (Kumpulainen et al. 2004, Elzinga et al. 2011b) contradicting theories for the predominance of sex (Muller 1964, Birky 1999, Rice & Friberg 2009). There is an additional interest in bagworm moths because parthenogenetic species evolved independently from different sexual ancestors (Grapputo et al. 2005a) and showed unexpected genetic diversity (Grapputo et al. 2005b).

For some species of bagworm moths (Narycinae) the task of species delimitation is extremely difficult when using traditional taxonomy, since most species look remarkably alike and share similar ecological characteristics. The minimal morphological differentiation that is observed in bagworm moths makes necessary the application of a DNA barcoding approach (Hebert et al. 2003). Accurate species identification is essential to test several hypotheses for the origin (paper II) and maintenance (paper III, paper V) of parthenogenetic reproduction. The first aim of this dissertation (paper I) was to implement the use of the currently standardized mitochondrial COI for species delimitation. In order to complement the goal of an accurate delimitation of species, the first pa-

per also included the comparison between morphological identification and the outcome from the DNA barcoding approach.

Currently, the processes and causes that generate and maintain parthenogenetic reproduction in bagworm moths remain unclear. Conclusive evidence concerning the hybrid or autopolyploid origin of *D. fennicella* is still lacking due to limited knowledge about ploidy levels and genome size in both parthenogenetic and sexual species. The second aim (paper II) was to evaluate the processes that potentially contributed to the evolution of *D. fennicella* in central Finland. Specifically, the second paper looked to determine whether parthenogenetic reproduction has originated either by i), hybridization events between two sexual species or ii), through autopolyploidization of a related sexual species. For this purpose, the second paper reports the ploidy level of bagworm species and describes an integrative approach consisting of phylogeny reconstruction of both mitochondrial and nuclear DNA.

In order to investigate the factors that contributed to the maintenance of parthenogenetic reproduction in *D. fennicella*, the third aim of this dissertation (paper III) was to determine whether wingless sessile females faced the risks of sperm limitation (Rhainds et al. 2009). This study examined the effects of male mating history on female fitness among closely related sexual species. The study of sperm limitation was of great importance, as it could have played a significant role in the evolution of parthenogenesis in bagworm moths.

Continuing to investigate the factors that might contribute to the maintenance of alternative reproductive strategies, the fourth aim (paper IV) was to test one of the predictions of the parasite hypothesis of sex. The parasitism levels of the parthenogenetic and sexual species were compared through molecular identification of the parasitized hosts. The prediction of the parasite hypothesis of sex states that parasitoids should preferentially attack parthenogenetic species in sites where they coexist with sexuals. As a result, parthenogens should be eliminated from a mixed population. However, previous ecological studies showed no signs of decline in reproduction or population viability of this species (Kumpulainen et al. 2004, Elzinga et al. 2011b). The fourth paper also focused on investigating the important prerequisite that "all else is equal," for testing the parasite hypothesis. This assumption states that there are no differences in life history between sexual and parthenogenetic forms (Schlupp & Tobler 2008), which may affect parasitism levels or reproductive success.

The assessment of the level of genetic variation in parthenogenetic species is essential to evaluate its evolutionary potential. Therefore, the isolation of microsatellites (paper V) was conducted in an attempt to elucidate alternative explanations for the lack of decline or viability in the populations of *D. fennicella*. Additionally, microsatellite markers were isolated to confirm the relatively high levels of genetic variation reported in allozymes (Grapputo et al. 2005b).

2 MATERIALS AND METHODS

2.1 Study Species

Bagworm moths (Lepidoptera: Psychidae) comprise a taxonomically diverse group with a worldwide distribution (Rhainds et al. 2009). Their common name makes reference to the fact that the larvae live and complete their development in a self–made case made of fragments of lichen, plants and other small particles (Rhainds et al. 2009). Females (Fig. 2) from the subfamily Naryciinae are wingless with a maximum length of 5 mm and the males (Fig. 2) have a wingspan of ca. 15 mm (Suomalainen 1980).

After overwintering, final instar larvae climb up trees to pupate. Larvae (Fig. 2) develop and pupate inside their case. The larvae of Naryciinae are often parasitized by eight species of hymenopteran parasitoids (Fig. 2) (Elzinga et al. 2011a). As other psychids, adults do not feed. Their lifespan is considerably short, as adults tend to live for approximately five days. In Finland, these species occur in boreal forest habitats where both sexual and parthenogenetic species coexist (Kumpulainen et al. 2004, Elzinga et al. 2011b). Five sexual species and two obligate parthenogenetic have been reported in central Finland (Elzinga et al. 2011b). The parthenogenetic moths *Dahlica fennicella* and *D. triquetrella* co–exist with closely related sexual species (Suomalainen 1980, Kumpulainen et al. 2004, Elzinga et al. 2011b). Parthenogenetic species are quite abundant and show no signs of decline or high parasitism (Fig. 3 & 4).

In early spring, last instar larvae climb up trees in order to pupate. Adults emerge within 2–4 weeks after the beginning of their pupal stage. A broad species classification can be made based on reproductive strategy. Parthenogenetic females start to lay eggs immediately after emergence, while sexual females release pheromones in a typical calling position and males are clearly sexuals. Sexual and parthenogenetic females lay their eggs inside their larval case, after which the female drops and perishes. Immediately after hatching, the larvae construct their own case. The larvae feed on lichen and moss. It seems that the species of bagworm moths have one to two year life cycle. In this dissertation I

focused to study the following species of Naryciinae occurring in Central Finland: two parthenogenetic species *Dahlica fennicella* and *D. triquetrella*, and five sexual species *D. charlottae, D. lazuri, D. lichenella, Sideria listerella* and *S. rupicolella* (Suomalainen 1980).

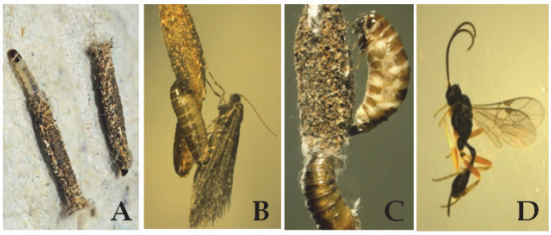

FIGURE 2 Bagworm moths. Larvae and their self made case (A), sexual (on mating position) (B), parthenogenetic bagworm moth (C) and a hymenopteran parasitoid (D).

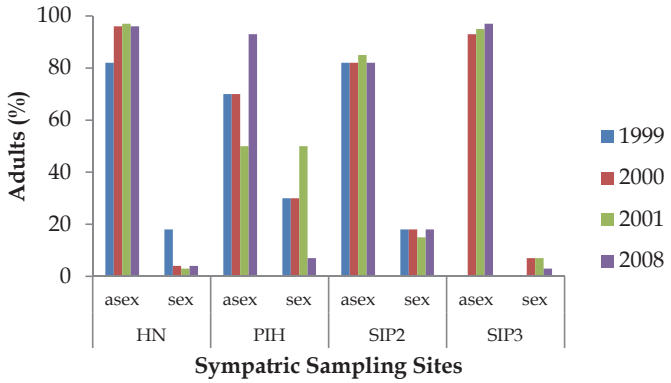

FIGURE 3 Ocurrence of parthenogens (asex) and sexuals (sex) in sympatric sites.

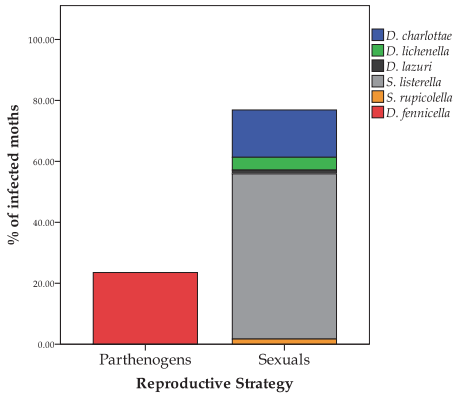

FIGURE 4 Percentage of parasitism of the parthenogenetic *D. fennicella* versus sexual species.

2.2 Field Sampling

In early March during 2007 to 2011, last instar larvae were collected by setting tape traps around tree trunks in a total of 70 forested sites. The sampling sites were located around the city of Jyväskylä, Central Finland and in nearby areas of Evo, Southern Finland. In 2008, field sampling was also conducted in Åland and Estonia (Fig. 5). At each site tape (TRENDtape, Müroll, Franztanz, Austria) was attached with the adhesive side outwards around tree trunks (*Picea* sp, *Betula* sp, *Pinus*, sp and *Populus* sp) approximately 1.5m above the ground. The maximum distance among trees within a site was 100m.

All the Naryciinae larvae that were trapped by the tape were collected (aprox 30.000). Each sampling site was visited once a week for two months. Additionally, in 2007 early instar larvae were collected and reared until fall.

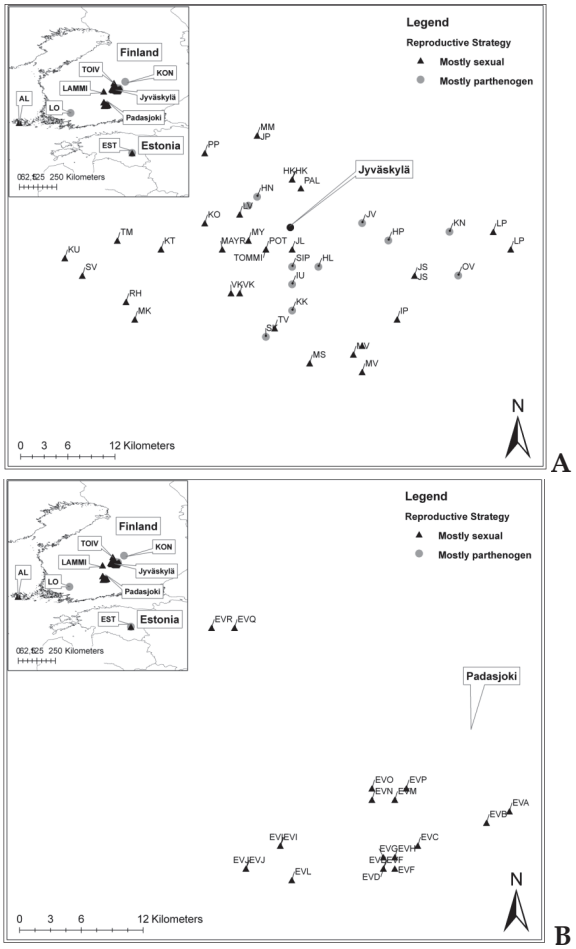

FIGURE 5 Sampling locations of bagworm moths in Åland, Estonia, Jyväskylä (A) and Evo village (B).

2.3 Laboratory rearing

At the beginning of the field season, all larval cases were kept in individual containers simulating field conditions at 10/20ºC (16/8 h cycle) and 85% humidity. A minority were kept at 5ºC for up to three weeks due to time and space constraints. From the beginning of July to early September, the temperature was set at 15/25ºC (16/8 h cycle) to simulate summer conditions. In early October the temperature was constant at 4ºC for five months to simulate winter conditions. The dark/light cycle in the growth cabinet was adjusted regularly to field conditions throughout the year.

All containers were checked on a daily basis for the emergence of moths or parasitoids. In case of pupal parasitoids, the gender of the moth pupa was determined based on the presence or absence of wing plates. Adult moths were placed in 99% ETOH for DNA barcoding (paper I), phylogenetic analysis (paper II) and microsatellite isolation (paper V). If a parasitoid emerged the remains of the host larva were collected and preserved in 99% ETOH for the identification of the host. DNA was extracted from the available larval remains collected in 2008 from sites where at least one parthenogenetic adult had emerged ('sympatric' sites). A DNA barcoding approach was used to determine the species of the larvae that were killed by parasitoids (paper IV). All parasitoids were identified based on morphology, for details refer to (Elzinga et al. 2011a). To check for a potential identification bias of DNA barcoding, the 209 larval remains from sites with over 75% of parthenogenetic adults were compared with 255 larval remains from sites with 100% of sexual adults. No parasitoids or moths emerged after the winter conditions. A subsample (n=42) of the cases from which nothing emerged was dissected in order to collect dead larvae or pupae.

2.4 Morphological Analyses

2.4.1 Males

Traditionally, morphological identification in bagworm moths was based on the genital index and on the shape of wing scales (Sauter 1956, Dierl 1966, Suomalainen 1980, Pro Natura 1997, Hauser 2004, Bengtsson et al. 2008). Paper I includes an analysis of the length of aedeagus, the valve, the traditional genital index and wing scale measurements in an attempt to discriminate the different species of bagworm moths with DNA barcoding.

Each right forewing was mounted dry on a microscope slide. The measurements were manually performed on a photograph that was taken of the distal ¾ of each wing, between the R2 and R3 veins, with a Zeiss Axioskop microscope with 10x magnification using the program SPOT v 4.0.1 (Diagnostic Instruments, Sterling Heights, MI). Several parameters were measured from each of the scales (Fig. 6): number of peaks, total length, partial length (a) that was

obtained by subtracting the total size of the scale from the peak length (b), width below peaks (c), and the width at 2/3 of total length (d). Six ratios were calculated from the measurements: a/b, a/c, a/d, b/c, b/d and c/d. The number of scales that were measured was variable (5–10) due to the fact that the scales frequently overlapped, which prevented some measurements.

In order to prepare microscope slides of the genitalia, the distal part of the abdomen was left overnight in a solution of 10% KOH to soften the surrounding tissues. On the next day, the genitalia were dissected and mounted in eupharal (ANSCO Laboratories, Manchester, England). Two measurements were manually taken: length of the aedeagus and the length of the two valve (Fig. 3). Subsequently, the average length of the two valve and the traditional genital index (ratio between the aedeagus length and the longest valve) was calculated (Suomalainen 1980). The measurements were obtained from a photograph taken with a Zeiss Axioskop microscope with 40x magnification using the program SPOT v 4.0.1 (Diagnostic Instruments, Sterling Heights, MI).

2.4.2 Females

Morphological identification of females has typically considered the shape of the capito–prosternal plate (Fig. 6) of the female pupa (Suomalainen 1980, Hattenschwiler 1985, Pro Natura 1997). Hauser (2004) also suggested an index between the length of the pupal antennal sheath and the length of the capito–prosternal plate. Several parameters were measured and calculated to determine whether the capito–prosternal plate of the pupa was useful for species delimitation of barcoded moths (paper I).

First, the capito–prosternal plate of the female pupa was mounted dry on a microscope slide. A photograph was taken using a stereomicroscope Olympus SZX9 with 12.5x magnification using the program Image Pro Plus v7.0 (Media-Cybernetics, Silver Springs, MD). Five measurements were manually performed on each photograph (Fig. 6): a–b (1), a–c (2), a–d (3), a–e (4) and the length of the pupal antennal sheath (f) (5). Next, the following ratios were calcutaed: 5/1, 5/2, 5/3, 5/4, 4/1, 4/2, 4/3, 3/1, 3/2 and 2/1. The 5/4 ratio corresponds to the index calculated by Hauser (2004).

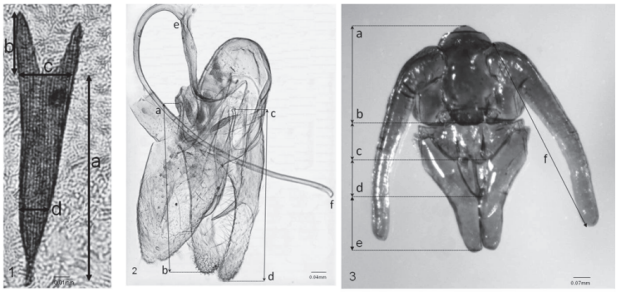

FIGURE 6 Morphological characters that were analyzed for seven species of Naryciinae (1) Wing scale measurements and ratios for males (2) Male genitalia measurements (3) Measurements of the capito–prosternal plate of the female pupa.

2.5 Molecular Analyses

2.5.1 Genome size and ploidy level

Flow cytometry measurements allowed us to determine ploidy level and genome size of parthenogenetic and sexual bagworm moths (paper II). Specimen tissue was taken and stained using the CyStain PI absolute T kit from Partec (Muenster, Germany) according to the manufacturer's instructions. We used heads of *Drosophila melanogaster* (Oregon–R strain) females as the size standard of known genome size.

The output files from the flow cytometry measurements (FCS files) were exported as text using WinMDI v 2.9 (Joseph Trotter, The Scripps Institute, La Jolla, CA) and pasted on an Excel (v. 14) sheet. Then, the mean fluorescence from the standard (*D. melanogaster*) and moth sample 2C (diploid) or 4C (tetraploid) peak was calculated. The mean of the peaks of interest was estimated avoiding cell clumps and debris. The moth sample and standard *D. melanogaster* peaks were confined by establishing their range, cut off range and cut off point.

DNA content for each moth species was calculated according to Tsutsui et al. (2008) as the ratio between the mean fluorescence 2C peak or 4C of the moth and the overall average (97.21 units) mean fluorescence 2C peak of *D. melanogaster*. This ratio was denominated "relative DNA" as it was not multiplied by the value of the genome size of *D. melanogaster*, as there is some variation on its estimation (Bennett et al. 2003, Gregory & Johnston 2008).

2.5.2 Amplification of mitochondrial and nuclear genes

DNA was extracted from sexual and parthenogenetic individuals using the QIAGEN DNeasy Blood & Tissue kit (QIAGEN, Hilden, Germany) according to the manufacturer's protocol and by eluting the DNA in 100ul of buffer AE.

The amplification of the partial sequence of the COI gene (657bp) was performed using the primer pair reported in (Wahlberg & Wheat 2008): LCO (fwd) G GTC AAC AAA TCA TAA AGA TAT TGG and HCO (rev) T AAA CTT CAG GGT GAC CAA AAA ATC A. The COII fragment (331bp) was amplified using the primer pair: COII–M1F (fwd) TT GGA TTT AAA CCC CAT YTA and C2–N–3389(rev) TCA TAA GTT CAR TAT CAT TG (Simon et al. 1994).

The partial sequence of the CAD gene (604 bp) was obtained with a Narycinae specific primer pair: psyCADF(fwd) TGGTAAAAATTCCAAGATGG and psyCADR(rev) ATCAAATTCGACAGAACTGC. The amplification of the fragment of the nuclear MDH (730 bp) was conducted using the primer pair reported in (Wahlberg & Wheat 2008): MDHF(fwd) G AYA TNG CNC CNA TGA TGG GNG T and MDHr(rev) AGN CCY TCN ACD ATY TTC CAY TT.

All PCR reactions were performed using the FailSafe PCR System (Epicentre Biotechnologies, Madison, Wisconsin) in a total reaction volume of 20 µl, that included 20–50 ng of DNA, 0.5 µM of forward and reverse primer, 10 µl of Buffer B 2X and 2.5 U/µl of Taq DNA Polymerase. Reaction conditions were as

follows: an initial denaturation step of 30s at 95°C, 30 cycles consisting of 30s at 95°C, 30s at 49–50°C annealing temperature (depending on primer combinations) and 1.5 min at 72°C followed by one cycle of 5 min at 72°C. The PCR products were verified by electrophoresis in agarose gel (1%). If there was a single band, the products were purified using Exonuclease I–Shrimp Alkaline Phosphatase (Amersham Biosciences). If more bands were visualized, the expected product was cut from the gel and purified with the QIAquick gel extraction kit from QIAGEN according to the manufacturer's instructions.

All the sequencing reactions were conducted with the BigDye® Terminator v3.1, Cycle Sequencing Kit (Applied Biosystems) using the M13 primers (0.2μM) and run on an ABI 3130xl Genetic Analyzer (Applied Biosystems). The primer pairs for the four genes had an M13 "tail" either forward 5'–TTGTAAAACGACGGCCAGT–3' or reverse 5'–CAGGAAACAGCTATGACC–3'.

The PCR products were sequenced on both strands, the sequences were edited for ambiguities in Seqscape v2.6 (Applied Biosystems). Subsequently, the sequences were aligned with ClustalW in MEGA v. 5 (Tamura et al. 2011) with default settings.

2.5.3 DNA barcoding

DNA barcoding initiative was initially developed by (Hebert et al. 2003). Nowadays, it is considered a rapid and cost effective molecular tool for species identification (Hausmann et al. 2011) based on genetic distances (Hebert et al. 2003, Pons 2006) and in the availability of reference sequences.

This popular technique is based on the amplification of a specific region of the DNA. Due to its high flexibility, the genetic material can be extracted from any type of tissue including all live stages of the organism that is being examined. The genomic region to be amplified varies according to the species. In insects, mitochondrial genes predominate for DNA barcoding (Roe & Sperling 2007, Rach et al. 2008, Yassin et al. 2010, Strutzenberger et al. 2011, Hausmann et al. 2011, Heethoff et al. 2011) due to their rapid evolution, maternal inheritance, robustness against degradation and limited recombination (Avise et al. 1987).
The identification of the species (papers II, III, IV and V) was only based on a barcoding approach using the partial sequence of the mitochondrial cytochrome II (COII). The reference sequences used were those reported in Grapputo et al. (2005a) and available in GenBank. The delimitation of the different species of bagworm moths was determined according to their clustering position in several groups that contained reference sequences. The NJ trees were based on the Kimura 2 parameter (K2P) model of nucleotide substitution (Kimura 1980) as recommended in the barcoding protocol (Ratnasingham & Hebert 2007). The trees were obtained using MEGA v. 5 (Tamura et al. 2011). The first paper also reports the use of the partial sequence of the COI as the standardized barcode (Fig. 7). Additionally, we used an identification approach based on direct sequence comparison to complement our results with those of the NJ trees using TaxonDNA/SpeciesIdentifier 1.7.7–dev3 (Meier et al. 2006).

The COI and COII sequences were evaluated according to the following criteria: "Best Close Match" and "All species barcodes." "Best Close Match" identifies the best barcode match of a sequence and assigns a species name to a query only if the barcode is sufficiently similar. In contrast, "All species barcodes" is more rigorous than the best close match criteria by using information from all conspecific barcodes in the data instead of focusing on the barcode that is similar to the query. Subsequently, we tested whether proposed distance thresholds for DNA barcoding, such as 1% (Ratnasingham & Hebert 2007) and 3% (Hebert et al. 2003) grouped the species of moths in the same clusters that were obtained in NJ trees.

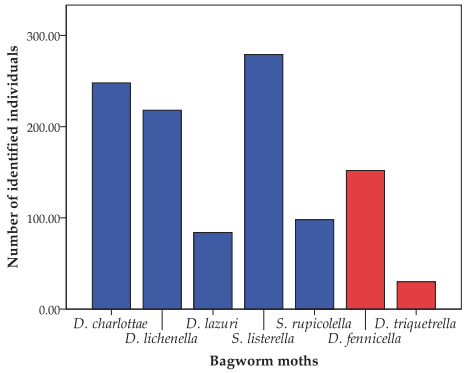

FIGURE 7 Identified bagworm moth species (n=1109) based on DNA barcoding of the COII (papers II, III, IV and V) and COI (paper I).

2.5.4 Phylogenetic Reconstruction

This analysis was conducted to determine the origin and phylogenetic relationships of the parthenogenetic moth *D. fennicella* (paper II). The phylogenetic reconstruction included the following species occurring in Central Finland (7 species): two parthenogenetic species *Dahlica fennicella* and *D. triquetrella*, and five sexual species *D. charlottae, D. lazuri, D. lichenella, Sideria listerella* and *S. rupicolella*.

Phylogenetic relationships were evaluated based on Bayesian inference (BI) (using MrBayes) and Maximum likelihood (ML) (using PhyML). Separate and concatenated gene trees were obtained for both methods. Concatenated gene trees were built in an attempt to get a more robust phylogenetic inference from mitochondrial and nuclear genes. However, this approach might violate the different evolutionary histories for each gene (Satler et al. 2011). For the nuclear genes, the heterozygous sites were left with the nucleotide ambiguity code (unphased). Ambiguous characters are treated as uncertain in MrBayes and ignored in PhyML as they do not carry any phylogenetic information.

The best–fit models for nucleotide substitution were obtained using jModelTest v 0.1.1 (Posada 2008). The models were based on the Akaike information criterion (AIC) (Posada & Crandall 1998). For the mitochondrial genes

we obtained the Kishino and Yano model (Hasegawa et al. 1985) with a proportion of invariable sites for COI (HKY + I) and with gamma rate variation for COII (HKY + Γ). The most suitable model for the CAD gene was the General time reversible model (Lanave et al. 1984) with gamma distributed rate variation across sites (GTR + Γ). The best model for the MDH was the symmetrical model (Zharkikh 1994) with a proportion of invariable sites and gamma distributed rate variation across sites (SYM+I+ Γ). A sequence of *Narycia duplicella* was included as an outgroup for all genes except for MDH, where a PCR amplification product was not obtained.

Bayesian phylogenetic trees were obtained for each gene separately (COI, CAD and MDH) and from concatenated gene sequences with MrBayes v 3.1 (Ronquist et al. 2005). Concatenated phylogenetic trees included mitochondrial (COI– COII) and nuclear genes (CAD–MDH). Two simultaneous independent runs with three heated chains and one "cold" chain were run for a number of generations that varied between 3 million and 10 million, with a sample frequency of 1000 and a burnin of 25% of the total number of samples. The default random tree and the contype = allcompat option were used at all times. The default of a random starting tree was always assumed, except for the concatenated nuclear genes where a user tree and ten perturbations were specified in order to reach convergence. The standard deviation of split frequencies (≤ 0.01) and the potential scale reduction factor (near 1.00) were used as the parameters for convergence (Hall 2011). The support of each cluster was evaluated following the criteria of (Hillis & Bull 1993), where a Bayesian posterior probability (BI) of ≥0.95 is considered to significantly support taxonomic relationships.

Phylogenetic relationships were also reconstructed using Maximum Likelihood. Separate and concatenated gene trees were estimated with PhyML (Guindon 2009). The separate gene trees were estimated based on the same models that were used for Bayesian inference. However, due to the limitation of the program to specify different substitution models for each gene in concatenated trees, we used the same model for mitochondrial (HKY+I+ Γ) and for nuclear (GTR+I+ Γ) genes. We did not observe major changes in tree topology by using different models based on low AIC values.

Phylogenetic tree topology was based on a SPR approach (subtree pruning and regrafting), while the branch support had a bootstrap test of 100 replicates. According to default settings, starting trees were based on BIONJ. A bootstrap value above 70% was considered to significantly support taxonomic relationships (Hillis & Bull 1993). All the phylogenetic trees were edited using MEGA v.5 (Tamura et al. 2011).

2.5.5 Microsatellite Isolation

For the microsatellite isolation (paper V), genomic DNA was extracted using the QIAGEN DNeasy Blood & Tissue kit from eight *D. fennicella* females from different sites around Jyväskylä, Finland. The microsatellites were isolated through an enriched genomic library as described in (Galarza et al. 2009) with some modifications of the protocol.

Briefly, a simultaneous restriction–ligation of genomic DNA was performed using RsaI and MseI restriction enzymes. Double stranded linker–adapter primers were added according to (Hamilton et al. 1999). Subsequently, ligated DNA was enriched by magnetic bead selection with a biotin–labeled probe mixture consisting of $(GA)_{12}$ and $(CATA)_8$ at 1µM each. Next, enriched DNA was eluted in 45µl dH_2O from the bead probes and concentrated by ethanol precipitation. PCR amplification of the two enrichments was performed, both enrichments were pooled and purified using QIAquick PCR purification kit (Qiagen). Approximately 60ng/µl of purified DNA was cloned using CloneJET™ PCR Cloning kit (Fermentas). A total of 368 positive clones were sequenced using the BigDye® Terminator v3.1, Cycle Sequencing Kit (Applied Biosystems) and run on an ABI 3130xl Genetic Analyser (Applied Biosystems). Primer pairs for 11 potential microsatellite loci were designed using Primer3 (Rozen et al. 2000).

To assess microsatellite polymorphism, ten individuals from the parthenogenetic species were selected from sites around Jyväskylä, Konnevesi and SE Estonia. For the sexual species, a total of 36 individuals were selected from 14 locations around Jyväskylä, Evo and from the Åland islands. We included geographically distant sites to maximize the chance to find possible genetic variation. PCR reactions were performed in 20µl total volume with approximately 50ng of DNA, 2mM of $MgCl_2$, 0.5µM of forward and reverse primer, 0.2mM of dNTP´s, 10X Dream Taq Buffer (Fermentas) and 5U/µl Dream Taq DNA polymerase (Fermentas). PCR conditions were: an initial denaturation of 5min at 95°C, 15 cycles of 30s at 95°C, 30s at 65°C with a decrement in the temperature of –1°C per cycle and 45s at 72°C. Next, 35 cycles consisting of 30s at 92°C, 30s at 50°C annealing temperature, 45s at 72°C, a final extension of 10 min at 72°C. PCR products were purified using QIAquick gel extraction kit (Qiagen).

Subsequently, we used a cloning approach to detect possible polymorphisms in the microsatellites fragments previously amplified by PCR. Approximately 60ng/µl of purified microsatellite amplicon was cloned using CloneJET™ PCR Cloning kit (Fermentas) following the manufacturer's protocol. A total of 954 positive clones for the two parthenogenetic species, were screened for inserts. For the sexual species, a total of 225 clones were screened. Only variable clones were sequenced as described above. As a relative index of variation (C), we calculated the fraction between the number of observed alleles within the number of clones sequenced.

2.6 Sperm limitation experiment

The effects of male mating history on female fitness were examined to determine if sperm limitation occurs (paper III). To include all sexual species, the experiment was divided into two parts. The first one included early species (mid March), while the second incorporated late species (early May). However, enough data to analyse the effects of mating history was only obtained for *S.*

listerella and *D. lichenella*. The low number of copulations obtained for *D. lazuri*, *D. charlottae*, and *S. rupicolella* reflects the availability of species in the sampling sites.

At the beginning of each experiment, 20 males were randomly selected from newly emerged individuals. Each male was placed inside a 30–ml Coulter counter cup. Subsequently a 1–day old virgin female, that was randomly selected, was offered to one of the males. If the male did not show interest to mate within 30 s, the female was then offered to a different male (in random order) until mating occurred or no copulation took place. Copulations took 3–10 min. The experiment was repeated until no more 1–day old females were available or all males had mated. All males, whether mated or not, recuperated for several hours at room temperature, and were then kept overnight at 4 °C until the following day. Newly emerged males were added to the experiment for each male that died during 14 days after an experimental period started. The experiment continued until the males died.

After copulation, individuals were separated to prevent a second mating attempt. Males that mated were not included until the next day. The number of multiple male copulations varied due to differences in the availability of individuals and the willingness of males to mate.

Mated females were transferred to the climate cabinet to complete oviposition. Contrary to the expectation that females were strictly monandrous, some assumed the calling position a day after copulation.

The cases containing eggs from the mated females were kept in a growth chamber for several weeks until the larvae emerged. Several measures of female reproductive success were conducted for each clutch, including realised fecundity (the total number of eggs laid by the female), fertility (the number of emerged larvae) and hatching success (the proportion of eggs that hatched). After death all the individuals were preserved in 99% ETOH.

2.7 Statistical Analyses

2.7.1 Morphology

An ANOVA was conducted of all measurements and ratios to determine whether morphological characters were as effective as DNA barcoding for species delimitation purposes (paper I). Nested ANOVA´s were performed for the wing scale measurements and ratios, as more than one scale was included per individual. Next, post–hoc tests were conducted (Dunnett or Tukey, depending on the variance homogeneity) to determine potential groups of species that could be differentiated based on the measurements that showed statistical significance.

Subsequently, an agglomerative hierarchical cluster analysis based on Euclidean distances was performed to identify homogeneous (Zibaee et al. 2008)

groups of moth species using the measurements and indexes. The cluster analysis is performed without an *a priori* classification of the individuals.

Finally, a Discriminant Analysis (DA) (Dapporto 2008) was conducted, in which an a priori sorting was made based on our barcoding classification. The aim of this analysis was to verify if males and females grouped according to the DNA barcoding classification taking into account all measurements and ratios. The importance of each variable was evaluated based on its correlation with the different discriminant functions. Wilks´ lambda was used to predict the significance of the functions. The linearity assumption and the homogeneity of variance–covariance matrices were tested by examining the matrix scatterplots for all variables (Leech et al. 2005). All analyses were conducted in PASW Statistics v. 18.00.

2.7.2 Genome size and ploidy level

The "relative DNA" ratio was used for the ANOVA and post– hoc tests. The aim was to determine possible differences in genome size among the sexual species (paper II). Additionally, an independent samples t test was performed to assess possible differences between parthenogenetic species. Finally, to express the genome size in Mb and pg the "relative DNA" was multiplied by the estimated value of genome size for *D. melanogaster* (175Mb and 0.18 pg) (Bennett et al. 2003). All the statistical analyses were conducted in PASW Statistics v. 18.00.

2.7.3 Mating Experiment

Interespecific copulations (7%) and individuals without successful DNA barcodes were excluded from the analysis. However, the male mating history included all the copulations.

Generalised linear models with a quasibinomial distribution were employed to test whether male mating history affected the proportion of successful copulations (paper III). Linear mixed models (function 'lme' in the 'nlme' package in R) were used to test for effects of male mating history on fecundity and fertility. Male was the random effect and the linear fixed effect included the number of previous successful (when at least five eggs were produced) copulations or male age at copulation. Similarly, generalized linear mixed models (function 'glme' in the'lme4' package in R) were used to analyze hatching success.

The correlation between female fitness (in the first successful male copulations) and the number of successful male copulations was investigated because a negative correlation can be expected if the transfer of sperm is costly for the male. Additionally, female fecundity, fertility, and hatching success were analyzed separately (per species) and only for successful copulations. Analyses were performed in R 2.10.1 (R Development Core Team, 2009). To test whether the sex ratios of the emerged sexual adults differed from 1:1 $\chi 2$ tests for each

population (with more than 10 emerged adults, n = 53) were performed followed by a sequential Bonferroni correction.

To look for temporal variation in the sex ratios, as observed in (Rhainds et al. 1999), collection and development times for males and females were analyzed with an ANOVA. This analysis was performed prior to species identification for all the sexual moths that we collected, and also for a group of random individuals identified to species.

2.7.4 Parasitism rates in *D. fennicella*

Frequency of the parthenogen *D. fennicella* was calculated from among the adult (non–parasitized) moths that hatched. The analysis included 70 forested sites in central Finland. Parasitism rates (paper IV) were calculated per site from the total number of cases from which an adult moth or parasitoid emerged. A generalised linear model with a quasibinomial error distribution (GLM) was used to examine the correlations between parasitism rates and the frequency of parthenogenetic adults.

The frequency of parthenogens among the identified hosts was calculated (for each sympatric site separately) to investigate whether parthenogenetic larvae are relatively more parasitized than sexuals. Next, these values were compared to the frequencies of parthenogens among the adult moths in a GLM (with site and sample type as explaining factors). Additionally, we investigated if the frequency of parasitized females (which may include parthenogens) was higher (among the parasitized pupae) than the frequency of females among non–parasitized emerged pupae.

The total frequency of parthenogens among the identified hosts was compared with the total frequency of parthenogens among the adults with a binomial test to investigate if certain parasitoid species have a preference to attack parthenogenetic moths.

An hypothetical parasitism rate (HP) for all sympatric sites was calculated to determine if the variation in parasitism was due to differences in phenology of final instar larvae between the parthenogenetic and sexual moths.

$$HPx = \frac{\sum_{i=1}^{9}(Psex_{week\ i} \times Ex_{week\ i})}{\sum_{i=1}^{9} Ex_{week\ i}}$$

with *Psex* the total parasitism rate observed in the sexual sites and *Ex* the number of emerged individuals (adults plus parasitoids) in site *x* per week *i*, and compared it to the observed parasitism rates.

GLM were performed in R 2.10.1 (R Foundation for Statistical Computing, Vienna, Austria) and all other analyses with IBM SPSS Statistics 19 (IBM Corporation, Armonk, New York).

3 RESULTS AND DISCUSSION

3.1 Identification criteria for bagworm moths (I)

Identifying one species from another is central to being able to develop further into deeper questions concerning evolutionary biology of any group. Morphological characteristics were examined to determine their effectiveness to distinguish some species of Naryciinae, compared to molecular methods. Wing scales measurements and ratios performed poorly as a morphological character for species delimitation in males. The wing scales analysis included *D. charlottae* (n =8), *D. lazuri* (n=10), *D. lichenella* (n=18), *S. listerella* (n=11), and *S. rupicolella* (n=6). By comparison, the aedeagus length and the genital index (Suomalainen 1980) were better characters for morphological species differentiation. The analysis of the male genitalia comprised *D. charlottae* (n =11), *D. lazuri* (n=10), *D. lichenella* (n=14), *S. listerella* (n=11), and *S. rupicolella* (n=13). However, male genitalia were not effective to differentiate the two species of the genus *Siederia*. Therefore, the use of morphology to correctly identify males is not perfect.

The female capito–prosternal plate was analyzed as well, including *D. charlottae* (n =13), *D. lazuri* (n=10), *D. lichenella* (n=12), *S. listerella* (n=9), and *S. rupicolella* (n=10), *D. fennicella* (n=12) and *D. triquetrella* (n=8). Those findings also suggest that the effectiveness of measurements and ratios of the capito–prosternal plate of the pupa were highly inaccurate for species delimitation purposes, despite its use in earlier studies (Suomalainen 1980, Pro Natura 1997). The parthenogenetic *D. triquetrella* was the only species that could be discriminated based on the ratio between the length of the pupal antennal sheath and the total length (Hauser 2004). However, *D. triquetrella* can also be distinguished based on quicker and less demanding characteristics such as reproductive strategy and the larval case shape (Suomalainen 1980). Moreover, the cluster and discriminant analyses based on morphological characters did not generate an accurate classification for either males or females.

Hybridization represents one alternative, but less likely scenario that might explain the occurrence of overlapping morphological characters. Alt-

hough interspecific matings occur in laboratory conditions between ♀*D. lazuri*–♂*D.lichenella*, ♀*D. lichenella*–♂*D. lazuri* and ♀*D.lichenella*–♂*S. rupicolella*, no supporting evidence based on phylogenetic reconstruction (paper II) suggests that hybridization occurs in the wild (Chevasco et al. in prep).

Species names for DNA barcoding followed those reported in Grapputo et al (2005a) that were based on mtDNA and traditional morphology. The species identification was based on sampling location, larval case and shape of wing scales for males, but no quantitative analysis was performed. The morphological identification matched with the mtDNA haplotypes for the parthenogens *D. fennicella* and *D. triquetrella*. However, Grapputo et al. (2005a) reported some mismatches between morphological and DNA–based approaches. For instance, the COII references for *S. rupicolella,* based on morphology, clustered with *S listerella* sequences, which confirms the overlap between the two species of the genus *Siederia* reported in this study. Grapputo et al. (2005a) relied on the morphological identification of the Finnish specimens. Therefore, those morphological determined *S. rupicolella* were referred to as *S. listerella*. Moreover, *D. lazuri* specimens based on morphology clustered with *D. charlottae* sequences. Grapputo et al. (2005a) considered the morphological identification of *D. lazuri* to be unreliable, thus those *D. lazuri* sequences were denominated as *D. charlottae*. Nevertheless, uncertainty has to be considered for species naming among *S. listerella*, *S. rupicolella*, *D. lazuri* and *D. charlottae*. Another issue arises for *D. lichenella*, which was only considered as parthenogenetic in Finland (Suomalainen 1980, Sobczyk 2011). Nonetheless, the occurrence of a sexual form denominated *D. lichenella fumosella* was reported as well (Suomalainen 1980). According to our preliminary classification based on the COII, the sexuals that we denominated as *D. lichenella* clustered together with Austrian *D. lichenella fumosella* (not shown) which is considered as a sexual form of the parthenogenetic *D. lichenella* (Pro Natura 1997). Throughout our sampling, the strictly parthenogenetic *D. lichenella* was never found. Regardless of the unresolved issues concerning morphological characters and the uncertainty of species naming, the taxonomic units described herein remain valid. What remains questionable is how well the morphology–based species descriptions and names match what this study and future molecular work will help to resolve.

Results from our molecular identification offered much more promise for specimen identification, especially given the unreliable nature of morphological characters. The molecular identification of each species was supported by NJ trees and K2P distances that are mainly used for DNA barcoding (Hebert et al. 2003). Equivalent species specific clusters were obtained based on the partial sequences of either of the subunits of the mitochondrial cytochrome oxidase gene (COI → 331bp COII→ 657bp). Even the short COII fragment proved to be useful for species delimitation purposes, despite some possible disadvantages: too small to provide enough nucleotide variation, misrepresentation of the intra and interspecific distances and might contain regions of unusual nucleotide divergence (Roe & Sperling 2007). The use of short DNA fragments (this study),

single nucleotide polymorphisms (SNP´s) or insertions/deletions (indels) has been recognized as DNA barcoding *sensu lato* (Valentini et al. 2009).

Tree based identification techniques might be particularly effective for bagworm moths. Although some ambiguity may exist for the exact names, there are without doubt seven species specific clusters: *D. fennicella*, *D triquetrella* (parthenogenetic) and five sexual species *D. lazuri, D. lichenella, S. rupicolella, D. charlottae*, *S. listerella* (sexuals).

The analysis was complemented with alternative identification criteria, such as "Best Close Match" and "All Species Barcodes" (Meier et al. 2006). The results demonstrated the better performance of a standardized barcode (COI), for which we did not observe any ambiguities and a low percentage (1.04%) of incorrect assignments. In contrast, the COII fragment showed ambiguous identifications (9.8%) and the highest percentage of incorrect assignments (1.96%).

The DNA barcoding approach is based on genetic divergence. Therefore, several distance threshold values have been proposed to establish species delimitation boundaries. Nevertheless, none of the suggested values of 1% (Ratnasingham & Hebert 2007) and 3% (Hebert et al. 2003) separated the species into seven clusters as indicated by the NJ tree. Therefore, the application of threshold limits might be artificial and not applicable to every species (Rubinoff 2006, Ward et al. 2009).

3.2 Origin of parthenogenesis in *D. fennicella* (II)

Because sexual reproduction is considered so central to evolutionary potential, the exceptions pose intriguing questions for evolutionary biology. Alternate mechanisms for generating genetic variability (such as polyploidy) are typically at the center of explanations for the success of parthenogens. Here we examine the evolution of parthenogenesis in bagworm moths (*D. fennicella*) by focusing on ploidy levels, genome size and phylogenetic reconstructions. The phylogenetic reconstructions included a total of 127 individuals from five sexual and two parthenogenetic species. The mitochondrial genes comprised the partial sequences of the COI (657bp) and the COII (331bp) from the cytochrome oxidase gene. The nuclear gene fragments incorporated the CAD (604 bp) and MDH (730 bp). The results showed the non hybrid origin of the parthenogenetic *D. fennicella* in this group of Lepidoptera.

Flow cytometry measurements confirmed that the parthenogenetic *D. fennicella* and *D. triquetrella* were tetraploids, while sexual species were diploids. The genome size of *D. charlottae* (n=151) (M=1.77, SD=0.09) was significantly smaller than *D. lichenella* (n=62) (M=2.21, SD=0.01) and *S. rupicolella* (n=45) (M=1.87, SD=0.06). In contrast, the genome sizes of S. *listerella* (n=31) (M=2.10, SD=0.08) and *D. lazuri* (n=43) (M=2.1, SD=0.14) did not differ significantly. The results also revealed that were no significant differences in genome size between the two parthenogenetic species *D. fennicella* (n=60) (M=4.03, SD=0.20) and *D. triquetrella* (n=12) (M=4.00, SD=0.21) $t_{(70)}= 0.45$, $p= 0.66$.

The phylogenetic analysis revealed some insights into the evolution of parthenogenetic reproduction for *D. fennicella*. According to the partial sequences of mitochondrial genes there was a single transition to parthenogenesis. In contrast, the nuclear MDH and the concatenated nuclear phylogenies revealed two possible transitions, while the CAD gene showed that the parthenogenetic *D. fennicella* clustered in the same group with the sexual *D. lazuri*. As a result, the evolution of asexuality in *D. fennicella* remains unresolved because we observed two possible evolutionary paths. One possible explanation for the different results obtained from nuclear and mitochondrial genes is dissimilar evolutionary histories of the gene fragments used. Conclusive evidence for the evolution of asexuality would need an extensive number of samples from *D. lazuri* and *D. fennicella*.

In the mitochondrial phylogenetic trees, the parthenogenetic *D. fennicella* was found to be the sister species of *D. lazuri*. The phylogenies based on nuclear genes showed that *D. fennicella* and *D. lazuri* did not form separate clusters in the CAD analysis. In contrast, the MDH showed that *D. fennicella* and *D. lazuri* had a paraphyletic status within the same cluster. The close phylogenetic relationship between parthenogenetic *D fennicella* and the sexual *D.lazuri* was also reflected by low interspecific pairwise distances. Mitochondrial gene fragments showed a 0.9% of divergence for COI to 1.5% for COII, whereas nuclear genes had 0% of divergence for CAD to 1.6% for MDH. In all phylogenetic reconstructions the sexual *D. lichenella* was the sister species to the group of *D. fennicella* and *D. lazuri*, and all three species always formed a monophyletic group. Additional support for species relatedness among *D. fennicella*, *D. lazuri* and *D. lichenella* was corroborated by low interspecific variation among mitochondrial and nuclear gene fragments (1.2% to 3.3% divergence).

The phylogenetic analysis supported a non–hybrid origin for *D. fennicella*. However, the presumable parent species could have been potentially missed by limiting the sampling sites to Finland and Estonia. An alternative, but speculative, explanation to clarify the origin of *D. fennicella* is that it might have originated by means of autopolyploidization of the closely related sexual *D. lazuri*.

The speculation for an autopolyploid origin is based on the fact that the sexual form of *D. triquetrella*, that occurs in Switzerland (Lokki et al. 1975) produces automictic diploids that may originate tetraploid parthenogenetic females through autopolyploidization (Lokki et al. 1975, Stenberg & Saura 2009). Unfortunately, there are no observations for the existence of automictic diploids in *D. lazuri*. Additional support for an autopolyploid origin in *D. fennicella* could be corroborated by the fact that *D. fennicella* is a tetraploid and had approximately twice as much relative DNA when compared with the sexual *D. lazuri*.

A whole genome duplication event (autopolyploidization) in *D. fennicella* would have helped to reduce extinction risks by creating mutational robustness, functional redundancy, and increased rates of evolution and adaptation (Crow & Wagner 2006). A polyploid organism has unique gene combinations due to a double set of chromosomes, high levels of heterozygosity and altered expression patterns (Parker Jr & Niklasson 2000). Whole genome duplication could be one explanation for the abundance of parthenogenetic species (Kum-

pulainen et al. 2004, Elzinga et al. 2011b). Additionally, polyploidy helps parthenogenetic species to violate the basic assumptions that higher mutational load or lower genotypic variation would be disadvantageous (Hörandl 2009).

3.3 Sperm limitation on female reproductive success (III)

Sperm limitation is an important factor that might contribute for the spread for parthenogenesis, especially in wingless and sessile sexual females. The mating experiment results were expected to show a decrease in female reproduction due to an increased number of male copulations, male inability to consume nutrients and a short lifespan. In agreement with the expectations, fecundity and fertility decreased by about 30% in *S. listerella* (n=27♂). In contrast, no decrease was observed in *D. lichenella* (n=27♂). These findings suggest that the negative effects of male mating history might not be strong in Naryciinae. The most likely scenario could be that selection preferred males that do not reduce sperm quality and quantity in a monandrous species. Further evidence comes from the fact that the size of the spermatophores is smaller in monandrous species if compared to polyandrous species (Hughes et al. 2000, Lauwers & Van Dyck 2006). These findings might also suggest small ejaculation sizes in some of the species of Naryciinae. Moreover, the findings of the mating experiment showed that unmated females tend to re–mate, even if the species of Naryciinae are considered strictly monandrous (Rhainds et al. 2005a). Females from both species (*S. listerella* and *D. lichenella*) were observed to assume a calling position after unsuccessful mating attempts, waiting for a new male to arrive. Furthermore, male limitation did not constitute a constraint as only few sites had significantly skewed sex ratios.

The results also revealed different conflicts over mating for two species of Naryciinae. In *S. listerella*, females might obtain higher fitness by mating with a virgin male, while males can increase their fitness by mating with multiple females. In contrast, *D. lichenella* females obtain higher fitness by mating with older males and males can invest less in sperm to live longer and mate multiple times. The observed results could be attributed to the only known difference between these two species, which is larval timing, since many ecological aspects of the Naryciinae are still unknown.

According to the results of (Grapputo et al. 2005a) parthenogenesis has evolved several times in Naryciinae. One scenario to explain the favorable spread of parthenogenesis was that sexual reproduction might incur extremely high costs in this group, due to male and/or sperm limitation (Kumpulainen et al. 2004). Nevertheless, the findings of this paper (III) did not give strong support to the idea that sperm limitation constitutes a selective force that might favor parthenogenetic reproduction in sessile females.

3.4 Parasitism rates in *D. fennicella* (IV)

The overall parasitism rate of all species was 26% with a range from less than 20% in March to over 80% in May. The identified larval skin remains included *D. charlottae* (n=37), *D. lazuri* (n=2), *D. lichenella* (n=10), *S. listerella* (n=129), and *S. rupicolella* (n=4) and *D. fennicella* (n=56). The most common parasitoid was *Trachyarus borealis* with a total parasitism rate of 9.2%.

The parasite hypothesis predicts that in populations where sexuals coexist with asexuals (sympatric sites) asexuals should be more susceptible to parasitoid attacks due to the lack of genetic diversity (Tobler & Schlupp 2008). In agreement with Kumpulainen et al. (2004) the results also indicated a strong positive correlation between the prevalence of sexual and the presence of parasitoids. However, our study contradicts the parasite hypothesis of sex because the majority of parasitoids attacked sexual hosts at a higher rate. Compared to the total parasitism rate, both *Meteorus affinis* and *Macrus parvulus* showed a positive correlation with the proportion of *D. fennicella*. Interestingly, parthenogenetic species are rarely attacked by *T. borealis*, which was responsible for most of the parasitism in our study. None of the parasitoid species showed a clear preference for *D. fennicella* as was expected if at least one species of parasitoid would be responsible for a potential decline in the number of parthenogens. In general, our findings showed that most species of parasitoids co–occur with parthenogens, but the parasitism rate was typically low. One possible explanation for the success of *D. fennicella* is that parasitoids are poorly (or not yet) adapted to take advantage of *D. fennicella,* as predicted by the parasite hypothesis (Jokela et al. 2009). Another (not mutually exclusive to previous explanation) possibility is that *D. fennicella* patterns of genetic diversity that could potentially generate novel or rare genotypes.

Our ecological observations in *D. fennicella*, which co–occurs with sexual species might indicate that the assumption of "all else equal" (Tobler & Schlupp 2008) is not fully met. "All else equal" states that sexuals and parthenogens should not differ in ecology, physiology or life history. If the "all else equal" assumption is not met, the parasitoid attacks might be affected by ecological and physiological factors than through the differences in reproductive mode. Nevertheless, this study found important differences in larval phenology that could affect the risk of being parasitized because larvae of sexual species were found over a longer time period than *D. fennicella*. *Dahlica fennicella* probably has one year life–cycle, whereas a two–year life–cycle seems to be dominant in sexual species. Future investigations might help to establish whether phenological differences play a significant role in parasitism rates.

The parasitoid hypothesis of sex does not explain the coexistence of sexual and parthenogenetic bagworm moths. According to this study, sexuals should deal with several costs: the production of males, mating, and parasitism. Parthenogenetic species may avoid the parasitoids due to a relatively high level of

genetic variation (Grapputo et al. 2005a) although it was still lower than the sexual species.

3.5 Patterns of genetic diversity in *D. fennicella* (V)

Considering the results of the low parasitism rates in *D. fennicella* (paper IV), and previously reported genetic variability (Grapputo et al. 2005b). This paper investigated the possibility of the occurrence of diversity based on microsatellite markers. The results revealed that nine out of eleven loci showed polymorphism in the parthenogenetic *D. fennicella* (n=11), whereas only three loci amplified for *D. triquetrella* (n=5), from which only one showed polymorphism. Conversely, five out of nine loci showed polymorphism for sexual species: *D. charlottae* (n=5), *D. lazuri* (n=8), *D. lichenella* (n=13), *S. listerella* (n=5), *S. rupicolella* (n=2). In all species, microsatellite polymorphism included variation in the number of repeats and insertions within the repeat motif. The observed genetic variation in *D. fennicella* (average C = 0.42) cannot be explained by outcrossing.

Genetic diversity in parthenogenetic species might reflect the consequences of recombination due to intermittent sex. Occasional sexual reproduction would offer the advantages of sex with reduced costs (D'Souza & Michiels 2010). Nonetheless, occasional sex in *D. fennicella* is highly unlikely because males have never been found (Suomalainen 1980), and parthenogenetic females lay eggs immediately after hatching. A second possible explanation for the genetic polymorphism observed in *D. fennicella* could be an alteration of the achiasmate oogenesis mechanism. However, this might not be the case since female lepidopterans that reproduce with automictic parthenogenesis and central fusion without recombination have achiasmate oogenesis with no crossing over (Stenberg & Saura 2009). A third scenario includes mutational processes. It is generally accepted that microsatellites show higher mutation rates (10^{-2}–10^{-6}) than coding genes (Li et al. 2002). Higher mutation rates constitute a feasible explanation for genetic polymorphism in *D. fennicella*. Nevertheless, the confirmation for the observed genetic diversity might be only due to the multiple sets of chromosomes (tetraploid status) of *D. fennicella*. Alternatively, negative frequency dependent selection could maintain diversity in asexuals (Weeks & Hoffmann 2008) increasing fitness of a genotype when it becomes rare. The idea of negative frequency selection could be supported by contradictory findings in the IV paper, which showed that sexual species suffered higher parasitism rates. In contrast, parthenogens avoid parasitoid attacks by having rare genotypes that might be constantly changing by a continuously generated genetic diversity due to polyploidy. A more speculative explanation includes the existence of a large number of separate parthenogenetic lines, as in the parthenogenetic moth *Ectoedemia argyropeza* (Menken & Wiebosch-Steeman 1988). In either case, the results support the idea that in this system parthenogens are not evolutionary dead–ends.

4 CONCLUSIONS

4.1 Origin of parthenogenetic reproduction

The occurrence of certain parthenogenetic species contrasts with the dominance of sexual reproduction. Current investigations that focus on the origin and evolution of alternative reproductive strategies carry important implications for understanding the predominance of sex by identifying their advantages and maintenance. The apparent success of certain parthenogens is linked to different modes of origin that may lead to high heterozygosity levels, including hybridization (Simon et al. 2003). Hybridization between closely related sexual species is one of the most commonly proposed causes for the origin of parthenogenesis. A hybrid origin is often linked with polyploidy in parthenogens.

High ploidy levels (polyploidy) can minimize the effects of deleterious mutations and the expression of mutational effects in parthenogenetic species (Richards 1997, Otto & Whitton 2000). Based on the results, the two species of parthenogenetic moths (*D. fennicella* and *D. triquetrella*) are tetraploids and might be able to take advantages from a polyploid state when coexisting with closely related sexual species.

In order to confirm or reject the hypothesis of a hybrid origin in parthenogenetic species, it is necessary to identify sexual species. However, species delimitation in bagworm moths is problematic due to overlapping morphological and ecological characteristics. Therefore, the biological species concept (BSC) and the morphospecies concept cannot be applied to these moths. Bagworm moths, though, are suitable for the application of the phylogenetic species concept (PSC) based on a DNA barcoding approach (paper I), which enables us to draw clearer conclusions about the origin of parthenogenesis.

By successfully identifying sexual species, we were able to determine that parthenogenetic reproduction in *D. fennicella* likely originated by one of two possible paths: a single transition (mtDNA) or multiple transitions (nDNA). Despite the lack of conclusive evidence in favor of single or multiple transitions to parthenogenesis, our results show that hybridization did not lead to the origin

of the tetraploid parthenogenetic *D. fennicella*. The results indicate the most plausible hypothesis to explain the origin of *D. fennicella* is an autopolyploidization event of a closely related sexual species, such as *D. lazuri*. The eventual, but speculative, loss of sex in *D. lazuri* might indicate evidence for new adaptations for some Naryciinae.

Cytogenetic studies or chromosome mapping would be required (Maniatsi et al. 2010) in order to discard an allopolyploid or autopolyploid origin of *D. fennicella*. Future investigations could also test the hypothesis suggested by (Chenuil et al. 1999). In the case of autopolyploidy, any genetic marker in the first tetraploid ancestor is represented by two copies (haploid state), whereas in case of allopolyploidy some markers could be absent or display only one copy (Chenuil et al. 1999). The model requires knowledge of the phylogeny of a species descending from the same tetraploidization event, together with the number of homogeneous copies present in each species for a set of neutral markers.

4.2 Maintenance of parthenogenesis

The occurrence of parthenogenetic species constitutes an intriguing paradox of evolutionary success without the renowned mechanisms for providing genetic variation. Traditionally, the absence of sex was regarded as a precursor to extinction. Maynard Smith (1978) considered that "…in the long run parthenogenetic species are doomed to extinction because of their inability to evolve..." Contrary to expectations, parthenogenetic species of bagworm moths might be flourishing without sex. Studies of systems where sexual and parthenogenetic species co–occur, such as bagworm moths, provide evidence for or against the mechanisms that play important roles in the maintenance of sex (Neiman and Schwander 2011). There are three points that need to be considered for the maintenance of parthenogenesis in this group of psychids.

First of all, according to the parasite hypothesis (Van Valen 1973), sex generates genetic diversity conferring advantages to individuals with rare genotypes. In contrast to sexual species, parthenogens should be more susceptible to infection because they are less likely to produce new genotypes due to the lack of recombination. The apparent success of *D. fennicella* was supported by the fact that parthenogenetic species are less vulnerable to the attacks of hymenopteran parasitoids (paper IV). On the other hand, sexual species were more vulnerable to attacks, which contradicts the prediction of the parasite hypothesis. Additional studies focused on the potential differences in genes mediating host–parasite interactions would help elucidate why sexuals appeared more prone to parasitoid attacks.

Polyploidy represents a second point to consider when evaluating mechanisms maintaining parthenogenesis because it allows for genetic diversity. The tetraploid status of *D. fennicella* (paper II) may potentially confer resistance to parasites (Tobler & Schlupp 2010). Moreover, based on computer simulations

M'Gonigle and Otto (2011) determined that diploid hosts tend to suffer a greater number of parasitoid attacks. Patterns of genetic diversity might help parthenogens to cope with parasitoid attacks, as the parasitoids will tend to attack the most common genotypes. Indeed, the parthenogenetic *D. fennicella* might be avoiding parasitoid attacks due to unexpected genetic diversity based on microsatellite markers (paper V).

Thirdly, sperm and male limitation could favor the spread of parthenogenetic reproduction for wingless and sessile sexual females. The findings from paper III showed that sexual females could re–mate in case of prior unsuccessful copulations. The ability to re–mate reduces the risk of remaining unfertilized and indicates that unfertilization risk might not be responsible for the spread of parthenogenetic reproduction in this group of Lepidoptera.

The absence of sex in *D. fennicella* might constitute an evolutionary advantage. The parthenogenetic moth *D. fennicella* avoids the overwhelming costs of sex, and its polyploidy status helps to cope with a higher mutational load. Therefore, it appears that polyploidy plays an important role in the maintenance of parthenogenesis in bagworm moths. An additional factor that might contribute to the persistence of parthenogens is the type of parthenogenesis. According to (Stenberg & Saura 2009) lepidopteran females such as *D. triquetrella* have automictic parthenogenesis with central fusion, together with achiasmate oogenesis that guarantees the maintenance of heterozygosity. This type of cytological mechanism makes meiotic parthenogens much more persistent than mitotic parthenogens. The retention of meiosis (Neiman & Schwander 2011) could also be interpreted as an explanation for the dominance of sex that is characterized by meiotic mechanisms.

Although sexual reproduction is often considered an invaluable component of evolutionary potential, more detailed investigations show asexuality may not be quite as limiting. Mathematical models show that sex does not necessarily increase variability, the resulting variability is not always beneficial, and sometimes evolution might not favour sex (Otto & Lenormand 2002). A more recent study by (Gorelick & Heng 2011) claims that sex is a constraint on epigenetic and genomic variation that limits adaptive evolution. Furthermore, some parthenogens do show genetic variation (Scali 2009, Beukeboom & Pijnacker 2000), which might be facilitated by polyploidy. Our study supports the reported correlation between high ploidy levels and parthenogenetic reproduction. Based on current evidence from the bagworm moths system, parthenogenetic species seem to prevail mainly due to high ploidy levels. Nevertheless, the importance of sex cannot be completely minimized since it seems that most of the time parthenogens originate from sexual forms retaining meiosis and diversity from their ancestral forms. In the bagworm system, parthenogens appear to overcome all the potential disadvantages from the lack of sex. However, the maintenance of sex in this system remains unresolved.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Näkökulmia partenogeneettisten ja seksuaalisesti lisääntyvien pussikehrääjien (Lepidoptera: Psychidae: Naryciinae) ekologiaan ja evoluutioon

Suvullinen eli seksuaalinen lisääntyminen on hallitseva lisääntymisen muoto läpi eläinkunnan. Suvullisen lisääntymisen tärkein etu suvuttomaan tai neitseelliseen lisääntymiseen verrattuna on rekombinaation kautta säilyvä geneettinen muuntelu. Partenogeneesillä eli neitseellisellä syntymisellä tarkoitetaan alkion syntymistä naaraspuolisesta sukusolusta ilman koiraspuolisen sukupuolisolun vaikutusta. Tätä ei pidä sekoittaa suvuttomaan lisääntymiseen joka tarkoittaa eliön lisääntymistä jakautumalla tai muulla tavalla niin, että syntyvä uusi yksilö on geneettinen kopio emoeliöstä. Partenogeneesissä voi siis tapahtua meioosi ja rekombinaatiota, jolloin tyttäret eivät ole välttämättä äitinsä tarkkoja kopioita. Partenogeneettisesti lisääntyvillä lajeilla geneettinen muuntelevuus on kuitenkin paljon vähäisempää kuin suvullisesti lisääntyvillä eliöillä, koska vain yhden yksilön genomi siirtyy seuraavaan sukupolveen. Koska vain geneettisesti muunteleva populaatio voi sopeutua muuttuvan ympäristön haasteisiin, suvuttomasti lisääntyvän lajin mahdollisuudet säilyä evolutiivisessa kilpajuoksussa suvullisesti lisääntyvien kanssa ovat teoreettisesti vähäinen, vaikka suvuton lisääntyminen onkin suvullista lisääntymistä tehokkaampaa. Tästä huolimatta tunnetaan suvuttomasti lisääntyviä eliöitä, joiden tiedetään säilyneen jopa satoja miljoonia vuosia. Jotta voisimme ymmärtää niitä etuja ja haittoja, joita suvuttomaan lisääntymiseen liittyy, pitää kysymystä lähestyä kokonaisvaltaisesti katsoen sekä lajien evoluutiohistoriaa että ekologiaa. Väitöskirjassani tutkin lajien geneettistä vaihtelua sekä molekyylibiologian että genomiikan menetelmin ja pyrin yhdistämään tämän tietämyksen lajien runsaussuhteisiin, ekologiaan ja käyttäytymiseen. Tutkimuskohteenani olivat pussikehrääjiä, erityisesti Psychidae-heimon *Dahlica*- ja *Siederia*-sukuihin kuuluvia lajeja. Nimensä pussikehrääjät ovat saaneet niiden toukkien tavasta kantaa mukanaan pussia, johon se voi piiloutua vihollisiltaan. Lajin toukat elävät toukkana puiden rungoilla ja tyvillä syöden sammalia ja jäkäliä. Suomessa elävistä pussikehrääjistä osa lisääntyy suvullisesti ja eräät lajit vain suvuttomasti. Näiltä suvuttomasti lisääntyviltä lajeilta ei tunneta lainkaan koiraita.

Tämän lajiryhmän tutkimusta hankaloittaa se, että lajit muistuttavat erittäin paljon toisiaan. Toistaiseksi ei ole pystytty löytämään varmaa menetelmää, joilla lajit pystyttäisiin erottamaan ulkonäön perusteella toisistaan. Lajit myös elävät samankaltaisissa elinympäristöissä, joten niiden ekologiaan perustuva lajinmääritys ei myöskään ole luotettava. Tämän tutkimuksen ensimmäinen haaste olikin pyrkiä selvittämään montako pussikehrääjälajia Suomessa todellisuudessa elää, ovatko lajit todellisia biologisia lajeja ja tukevatko eri menetelmiin perustuvat lajimääritelmät toisiaan.

Väitöskirjassani keräsin näytteitä vuosina 2007-2011 yhteensä 70 populaatiosta ja tutkin pussikehrääjien morfologisia piirteitä ja vertasin morfologisista mitoista saatua erotteluaineistoa DNA-viivakoodausaineistoon. DNA-viivakoo-

daus (DNA Barcoding) on verrattain uusi molekyylibiologinen keino lajien tunnistamiseen. Viivakooditettavat geenialueet ovat lyhyitä genomin osia, jotka ovat lajin sisällä lähes samankaltaisia mutta muuntelevat lajien välillä. Morfologisista piirteistä käytin muun muassa siipisuomujen muotoa ja kokoa sekä genitaalien kokoa ja muotoa. Tärkein havaintoni oli se, etteivät morfologiset piirteet pystyneet erottamaan yksiselitteisesti lajeja vaikka DNA-viivakoodaus selkeästi löysi 7 erillistä lajia, joista kaksi havaintojeni mukaan lisääntyy suvuttomasti ja viisi suvullisesti. Nämä havainnot poikkeavat aiemmista tutkimuksista, jotka perustuivat joko ainoastaan morfologiseen aineistoon tai pelkästään geneettiseen aineistoon. Molekyylibiologiset menetelmät ovat toistaiseksi ainoa tunnettu keino erottaa pussikehrääjälajit luotettavasti toisistaan ja pussikehrääjille näyttää fylogeneettinen (evolutiivinen) lajimääritelmä sopivan paremmin kuin biologinen lajimääritelmä. Kirjallisuudessa ja geenipankissa annettuihin pussikehrääjien nimiin on kuitenkin syytä suhtautua varauksella. On mahdollista, että vaikka aiemmissa tutkimuksissa on käytetty samaa lajinimeä tutkimuskohteista, kyseessä ovat olleet eri lajit.

Koska partenogeneettinen lisääntyminen on erittäin harvinaista perhosilla, on aiheellista kysyä, miten se on kehittynyt pussikehrääjillä ja minkälaiset valintapaineet ylläpitävät sitä. Yksi merkittävämpiä partenogeneettisen lisääntymisen etuja suvulliseen lisääntymiseen verrattuna on, ettei partenogeneettisen lajin tarvitse investoida resursseja puolison etsimiseen ja paritteluun. Erityisesti lajeilla, joilla toinen tai molemmat sukupuolet ovat huonosti liikkuvia tai koiraita on vähän saatavilla, voi sperman riittämättömyys hedelmöittämään populaation kaikki naaraat olla merkittävä kustannus. Näin on arveltu olevan myös pussikehrääjillä, joilla saadut tutkimustulokset ovat viitanneet siihen, että naaras voi jäädä ilman parittelua johtuen koiraiden ajallisesta tai paikallisesta vähyydestä. Naaras voi myös jäädä ilman spermaa, mikäli parittelee koiraan kanssa, joka on paritellut jo aiemmin. Tulokseni kuitenkin osoittavat, että sperman riittävyys ei ole niin suuri ongelma pussikehrääjillä kuin aiemmat tutkimustulokset antavat ymmärtää. Ainoastaan yhdellä lajilla (*D. listerella*) hedelmöittymistodennäköisyys laski mikäli naaras paritteli koiraan kanssa, joka oli jo aiemmin paritellut. Pidän siis epätodennäköisenä, että sperman riittävyys olisi riittävä valintatekijä, joka olisi suosinut partenogeneesiä pussikehrääjillä.

On mahdollista, että puhtaasti geneettiset tekijät ovat johtaneet partenogeneesiin pussikehrääjillä. Kasveilla polyploidia, eli mutaatio, jossa peruskromosomistoja on useampi kuin kaksi on hyvin yleistä. "Ylimääräiset" kromosomistot voivat olla peräisin samasta (autopolyploidia) tai eri lajista (allopolyploidia). Eläimillä polyploidian on aiemmin uskottu olevan erittäin harvinaista. Testasin hypoteesia, että pussikehrääjien partenogeneesi olisi kehittynyt kahden lajin risteytymisen kautta, ja tämä olisi puolestaan johtanut kromosomiston kahdentumiseen (alloplyploidiaan) ja partenogeneesiin. Tutkimukseni vahvistivat sen, että partenogeneettinen *D. fennicella* on tetraploidi, eli sillä on kaksinkertainen kromosomisto. *D. fennicellan* kromosomisto on kuitenkin peräisin vain yhdestä lajista, eli kyseessä on autopolyploidia. Todennäköisin alkuperälaji *D. fennicellalle* on *Dahlica lazuri*, joka asettuu pussikehrääjien

evoluutiopuussa lähimmäksi *D. fennicella* -lajia. Tämä laji on diploidi. Kirjallisuuteen perustuvat aineistot osoittavat, että vastoin aikaisempia oletuksia polyploidia näyttää olevan usein yhteydessä myös eläinten partenogeneesiin. Onkin mahdollista, että moninkertainen genomi puskuroi tehokkaammin haitallisten mutaatioiden ilmenemistä.

Koska suvuttomasti lisääntyvillä eliöillä geneettinen muuntelevuus on vähäisempää kuin suvullisesti lisääntyvillä eliöillä, ennustetaan niiden olevan alttiimpia taudeille ja loisille. Pussikehrääjillä tavataan runsaasti pistiäisiin kuuluvia loisia. Loisittuja pussikehrääjiä voi olla populaatiosta jopa 30%. Sekä aiemmissa tutkimuksissa että omassani on havaittu loisten olevan yleisimpiä yhteisöissä, joissa on runsaasti suvullisesti lisääntyviä lajeja. Tämän tuloksen on arveltu tukevan niin kutsuttua punaisen kuningattaren hypoteesista johdettua ”loiset ja suvullinen lisääntyminen” –hypoteesia. Tämän hypoteesin mukaan loiset sopeutuvat yleisimpään genotyyppiin populaatiossa, jolloin harvinaisimmat genotyypit, joihin loiset eivät eksy, saavat valintaedun. Mikäli geneettinen muuntelu on vähäistä, kuten suvuttomasti lisääntyvillä lajeilla, loiset tappavat hypoteesin mukaan ne nopeasti sukupuuttoon. Aikaisemmissa tutkimuksissa ei ole pystytty osoittamaan edustivatko loisitut uhrit suvullisesti vai suvuttomasti lisääntyviä lajeja, koska loiset tappavat aina isäntänsä tunnistamattomaksi. Aikaisemmin pystyttiin tutkimaan ainoastaan loisten hyökkäyksiltä selviytynyttä populaatiota. Väitöskirjassani onnistuin ottamaan riittävän määrän näytteitä loisitun pussikehrääjän jäänteistä ja DNA-viivakoodausta apuna käyttäen määritin sekä loisen että isännän lajin. Tutkimukseni osoitti, että vastoin ennusteita ja aikaisempia arvioita, loiset suosivat suvullisesti lisääntyviä lajeja. Tätä yllättävää tulosta saattavat selittää sekä geneettiset että ekologiset syyt. Vaikka suvullisesti ja suvuttomasti lisääntyvät pussikehrääjälajit ovat ekologisesti ja morfologisesti hyvin samanlaisia, niistä löytyi kuitenkin joitain eroja. Suurin ero suvullisten ja suvuttomien pussikehrääjien välillä lienee se että suvuttomilla lajeilla on pääsääntöisesti yksivuotinen elinkierto. Tämän ansiosta partenogeneettiset lajit ovat alttiina loisille vähemmän aikaa verrattuna suvullisiin lajeihin. Tämä ero saattaa olla yksi selittävä tekijä seksuaalisten lajien suurempaan loistaakkaan.

Toinen hyvin yllättävä tulos oli, että partenogeneettisen *D. fennicella* -pussikehrääjän geneettinen monimuotoisuus oli paljon suurempi kuin mitä suvuttomasti lisääntyvältä lajilta voisi odottaa. *D. fennicellan* geneettinen vaihtelevuus saattaa olla syy siihen, miksi loisriski on pieni. Partenogeneettisen lajin geneettistä muuntelua voi selittää suuri mutaatiotiheys. Todennäköisempi vaihtoehto kuitenkin on, että kyseessä on niin kutsuttu automiktia, jossa ensin tapahtuu tumien yhtyminen ja kromosomiluvun puoliintuminen, mutta diploidi (tässä tapauksessa tetraploidi) luku palautuu kun kaksi haploidia (tässä tapauksessa diploidia) tumaa yhtyy. Tämän tyyppisessä partenogeneesissä heterotsygotian säilyminen on mahdollista.

Väitöskirjatyöni antaa uutta tietoa huonosti tunnettujen pussikehrääjien genetiikasta, evoluutiohistoriasta, taksonomiasta ja ekologiasta. Väitöskirjani valottaa ymmärrystämme suvullisen ja partenogeneettisen lisääntymisen evo-

luution mysteeristä. Osoitan väitöskirjassani, että *D. fennicella* partenogeneettisestä lisääntymisstrategiastaan huolimatta ei kärsi loistaakasta ja sen geneettinen monimuotoisuus on riittävän suuri kilpailemaan suvullisesti lisääntyvien lajien kanssa. Tulevaisuuden haaste on ratkaista, miten on mahdollista että hitaammin lisääntyvät ja loisten vaivaavat suvullisesti lisääntyvät pussikehrääjät pystyvät kilpailemaan ja säilymään yhteisöissä partenogeneettisten lajien kanssa. Evoluutiobiologian ”kuningatarmysteeri” suvullisen lisääntymisen säilymisestä jäi siis ratkaisematta.

REFERENCES

Asker S.E. & Jerling L. 1992. *Apomixis in plants.* CRC Press Inc, Boca Raton, Florida United States of America.

Avise J.C., Arnold J., Ball R.M., Bermingham E., Lamb T., Neigel J.E., Reeb C.A. & Saunders N.C. 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annu. Rev. Ecol. Syst.* 18: 489–522.

Barton N.H. & Charlesworth B. 1998. Why sex and recombination? *Science* 281: 1986–1990.

Bell G. 1982. *The masterpiece of nature: the evolution and genetics of sexuality.* Biddles Ltd, Guildford and King´s Lynn, Great Britain.

Bengtsson B.Å., Palmqvist G. & Johansson R. 2008. *Nationalnyckeln till Sveriges flora och fauna (= Encyclopedia of the Swedish Flora and Fauna), DE 1–13. Fjärilar: Käkmalar – säckspinnare. Lepidoptera: Micropterigidae– Psychidae.* Artdatabanken, Sveriges lantbruksuniversitet, Uppsala.

Bennett M.D., Leitch I.J., Price H.J. & Johnston J.S. 2003. Comparisons with *Caenorhabditis* (~ 100 Mb) and *Drosophila* (~ 175 Mb) using flow cytometry show genome size in *Arabidopsis* to be~ 157 Mb and thus~ 25% larger than the *Arabidopsis* Genome Initiative estimate of~ 125 Mb. *Ann. Bot.* 91: 547–557.

Bernstein C. 1998. Sex as a response to oxidative damage. In: Okezie I. & Halliwell B., (eds.), DNA & Free Radicals. Techniques, mechanisms, & applications. , OICA international, Saint Lucia, London, pp. 99–118.

Beukeboom L.W. & Pijnacker L.P. 2000. Automictic parthenogenesis in the parasitoid Venturia canescens (Hymenoptera: Ichneumonidae) revisited. *Genome* 43: 939–944.

Bicknell R.A. & Koltunow A.M. 2004. Understanding apomixis: recent advances and remaining conundrums. *Plant Cell* 16: 228–245.

Birky C.W., Wolf C., Maughan H., Herbertson L. & Henry E. 2005. Speciation and selection without sex. *Hydrobiologia* 546: 29–45.

Birky C. 1999. An even broader perspective on sex and recombination. *J Evol Biol* 12: 1013–1016.

Blackman R.L., Spence J.M. & Normark B.B. 2000. High diversity of structurally heterozygous karyotypes and rDNA arrays in parthenogenetic aphids of the genus *Trama* (Aphididae: Lachninae). *Heredity* 84: 254–260.

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

Carman J. 2007. Do duplicate genes cause apomixis. In: Hörandl E., Grossniklaus U., van Dijk P. & Sharbel T. (eds.), Apomixis: Evolution, mechanisms and perspectives., ARG Gantner Verlag KG, Lichtenstein, pp. 169–194.

Chenuil A., Galtier N. & Berrebi P. 1999. A test of the hypothesis of an autopolyploid vs. allopolyploid origin for a tetraploid lineage: application to the genus *Barbus* (Cyprinidae). *Heredity* 82: 373–380.

Chevasco V., Elzinga J.A., Viinikainen S.M., Mappes J. & Galarza J.A. 2012. Unexpected genetic variability in the parthenogenetic bag worm moth *Dahlica fennicella* (Lepidoptera: Psychidae) revealed by novel microsatellite markers. *Conserv. Genet. Resour.* 4: 159–162.

Choleva L., Janko K., De Gelas K., Bohlen J., Šlechtová V., Rábová M. & Ráb P. 2012. Synthesis of clonality and polyploidy in vertebrate animals by hybridization between two sexual species. *Evolution*.

Comai L. 2005. The advantages and disadvantages of being polyploid. *Nat. Genet.* 6: 836–846.

Crow J.F. 1999. The omnipresent process of sex. *J. Evol. Biol.* 12: 1023–1025. Crow K.D. & Wagner G.P. 2006. What is the role of genome duplication in the evolution of complexity and diversity? *Mol. Biol. Evol.* 23: 887-892.

Daly M. 1978. The cost of mating. *Am. Nat.* 112: 771–774.

Dapporto L. 2008. Geometric morphometrics reveal male genitalia differences in the *Lasiommata megera/paramegaera* complex (Lepidoptera, Nymphalidae) and the lack of a predicted hybridization area in the Tuscan Archipelago. *J. Zool. Syst. Evol. Res.* 46: 224–230.

Darwin C. 1859. On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life [reprinted 1964]. *Cambridge (MA): Harvard University* .

Delmotte F., Sabater-Muñoz B., Prunier-Leterme N., Latorre A., Sunnucks P., Rispe C. & Simon J.C. 2003. Phylogenetic evidence for hybrid origins of asexual lineages in an aphid species. *Evolution* 57: 1291–1303.

Dierl W. 1966. Zur Kenntnis einiger *Solenobia*–Arten (Lepidoptera: Psychidae). Ein Beitrag zur Fauna Bavarica. *Mitteilungen der Münchener Entomol. Ges.* 56: 190–196.

D'Souza T.G. & Michiels N.K. 2010. The costs and benefits of occasional sex: theoretical predictions and a case study. *J. Hered.* 101: S34.

Elzinga J.A., Zwakhals K., Mappes J. & Grapputo A. 2011a. The parasitoid species complex associated with sexual and parthenogenetic Naryciinae (Lepidoptera: Psychidae): Integrating ecological and molecular analyses. *Eur. J. Entomol.* 108: 635–650.

Elzinga J.A., Chevasco V., Grapputo A., & Mappes J. 2011b. Influence of male mating history on female reproductive success among monandrous Naryciinae (Lepidoptera: Psychidae). *Ecol. Entomol.* 36: 170–180.

Fisher R.A. 1958. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

Foighil D.O. & Smith M.J. 1995. Evolution of Asexuality in the Cosmopolitan Marine clam *Lasaea*. *Evolution* 49: pp. 140–150.

Galarza, J.A., Boulay, R., Cerda, X., Doums, C., Federici, P., Magalon, H., Monnin, T., Tico, C. 2009. Development of single sequence repeat markers for the ant *Aphaenogaster senilis* and cross species amplification in *A–iberica*, *A. gibbosa*, *A–subterranea* and *Messor maroccanus*. *Conserv. Genet.* 10: 519–521.

Gandon S. & Otto S.P. 2007. The evolution of sex and recombination in response to abiotic or coevolutionary fluctuations in epistasis. *Genetics* 175: 1835–1853.

Gorelick R. & Heng H.H.Q. 2011. Sex reduces genetic variation: a multidisciplinary review. *Evolution* 65: 1088–1098.

Grapputo A., Kumpulainen T. & Mappes J. 2005a. Phylogeny and evolution of parthenogenesis in Finnish bagworm moth species (Lepidoptera: Psychidae: Naryciinae) based on mtDNA–markers. *Ann. Zool. Fennici* 42: 141–160.

Grapputo A., Kumpulainen T., Mappes J. & Parri S. 2005b. Genetic diversity in populations of asexual and sexual bag worm moths (Lepidoptera: Psychidae). *BMC Ecology* 5: 1–11.

Gregory T. & Johnston J. 2008. Genome size diversity in the family Drosophilidae. *Heredity* 101: 228–238.

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

Guindon S.G., O. 2009. Estimating maximum likelihood phylogenies with PhyML. *Syst. Biol.* 5: 696–704.

Hall B. 2011. *Phylogenetic trees made easy: a how–to manual.* Sinauer Associates, Inc Publishers, Sunderland, Massachusetts U.S.A.

Hamilton, MB., Pincus, El., Di Fiore, A., Flesher, R.C. 1999. Universal linker and ligation procedures for construction of genomic DNA libraries enriched for microsatellites. *Biotechniques* 27: 500–507.

Harshman L.G. & Futuyma D.J. 1985. The origin and distribution of clonal diversity in *Alsophila pometaria* (Lepidoptera: Geometridae). *Evolution* 39: 315–324.

Hasegawa M., Kishino H. & Yano T. 1985. Dating of the human–ape splitting by a molecular clock of mitochondrial DNA. *J Mol Evol* 22: 160–174.

Hauser E. 2004. Vergleichende Morphologie ausgewählter Arten der Gattung *Dahlica* ENDERLEIN 1912 (*D.fumosella*, *D. lichenella*. *D. fennicella*, *D. charlottae*) mit einem Vermerk zu *Solenobia norvegica* (Lepidoptera, Psychidae). *Denisia* 13: 305–316.

Hausmann A., Haszprunar G. & Hebert P.D.N. 2011. DNA barcoding the Geometrid fauna of Bavaria (Lepidoptera): successes, surprises, and questions. *PloS one* 6: e17134.

Hebert P.D.N., Cywinska A., & Ball S.L. 2003. Biological identifications through DNA barcodes. *Proc. R. Soc. Lond. B Biol. Sci.* 270: 313–321.

Heethoff M., Laumann M., Weigmann G. & Raspotnig G. 2011. Integrative taxonomy: Combining morphological, molecular and chemical data for species delineation in the parthenogenetic Trhypochthonius tectorum complex (Acari, Oribatida, Trhypochthoniidae). *Front. Zool.* 8: 2.

Heethoff M., Norton R.A., Scheu S. & Maraun M. 2009. Parthenogenesis in oribatid mites (Acari, Oribatida): evolution without sex. *Lost Sex* : 241–257.

Hillis D.M. & Bull J.J. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst. Biol.* 42: 182.

Holliday R. 1988. A possible role for meiotic recombination in germ line reprogramming and maintenance. In: Michod R. & Levin B. (eds.), The Evolution of Sex, Sinauer Ass, Massachusetts, USA, pp. 45–55.

Hörandl E. 2009. A combinational theory for the maintenance of sex. *Heredity* 103: 445–457.

Hughes L., Siew–Woon Chang B., Wagner D. & Pierce N.E. 2000. Effects of mating history on ejaculate size, fecundity, longevity, and copulation duration in the ant–tended lycaenid butterfly, Jalmenus evagoras. *Behav. Ecol. Sociobiol.* 47: 119–128.

Innes D.J. & Hebert P.D.N. 1988. The origin and genetic basis of obligate parthenogenesis in *Daphnia pulex*. *Evolution* 42: 1024–1035.

Johnson S.G. 2006. Geographic ranges, population structure, and ages of sexual and parthenogenetic snail lineages. *Evolution* 60: 1417–1426.

Johnstone R.A. & Keller L. 2000. How males can gain by harming their mates: sexual conflict, seminal toxins, and the cost of mating. *Am. Nat.* 156: 368–377.

Jokela J., Dybdahl M.F. & Lively C.M. 2009. The Maintenance of Sex, Clonal Dynamics, and Host-Parasite Coevolution in a Mixed Population of Sexual and Asexual Snails. *Am. Nat.* 174: S43–S53.

Jokela J., Lively C.M., Dybdahl M.F. & Fox J.A. 1997. Evidence for a cost of sex in the freshwater snail Potamopyrgus antipodarum. *Ecology* 78: 452–460.

Kearney M., Fujita M.K. & Ridenour J. 2009. Lost sex in the reptiles: constraints and correlations. In: Schön I., Martens K. & van Dijk P. (eds.), Lost Sex. The evolutionary Biology of Parthenogenesis. . First ed., Springer Science + Business Media, Dordrecht The Netherlands, pp. 447–474.

Kimura M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J. Mol. Evol.* 16: 111–120.

Kokko H. & Mappes J. 2005. Sexual selection when fertilization is not guaranteed. *Evolution* 59: 1876–1885.

Kondrashov A.S. 1988. Deleterious mutations and the evolution of sexual reproduction. *Nature* 336: 435–440.

Kondrashov A. 1993. Classification of hypotheses on the advantage of amphimixis. *J. Hered.* 84: 372–387.

Kondrashov F.A. & Kondrashov A.S. 2001. Multidimensional epistasis and the disadvantage of sex. *Proc. Natl. Acad. Sci.* 98: 12089.

Kumpulainen T. 2004. The evolution and maintenance of reproductive strategies in bag worm moths (Lepidoptera: Psychidae). PhD thesis, University of Jyväskylä, Finland.

Kumpulainen T., Grapputo A. & Mappes J. 2004. Parasites and sexual reproduction in psychid moths. *Evolution* 58: 1511–1520.

Lanave C., Preparata G., Sacone C. & Serio G. 1984. A new method for calculating evolutionary substitution rates. *J. Mol. Evol.* 20: 86–93.

Lauwers K. & Van Dyck H. 2006. The cost of mating with a non–virgin male in a monandrous butterfly: experimental evidence from the speckled wood, Pararge aegeria. *Behav. Ecol. Sociobiol.* 60: 69–76.

Leech N.L., Barrett K.C. & Morgan G.A. 2005. *SPSS for intermediate statistics: Use and interpretation.* Lawrence Erlbaum Associates, Inc, Publishers, New Jersey, USA.

Lehtonen J., Jennions M.D. & Kokko H. 2011. The many costs of sex. *Trends Ecol. Evol.* 27: 172–178.

Li Y.C., Korol A.B., Fahima T., Beiles A. & Nevo E. 2002. Microsatellites: genomic distribution, putative functions and mutational mechanisms: a review. *Mol. Ecol.* 11: 2453–2465.

Lively C.M. 1996. Host–parasite coevolution and sex. *Bioscience* 46: 107–114. Lively C.M. 2010. A review of Red Queen models for the persistence of obligate sexual reproduction. *J. Hered.* 101: S13–S20.

Lokki J., Suomalainen E., Saura A. & Lankinen P. 1975. Genetic polymorphism and evolution in parthenogenetic animals. II. Diploid and polyploid *Solenobia triquetrella* (Lepidoptera: Psychidae). *Genetics* 79: 513.

Mable B. 2004. "Why polyploidy is rarer in animals than in plants": myhts and mechanisms. *Biol. J. Linn. Soc.* 82: 453–466.

Malik S.B., Pightling A.W., Stefaniak L.M., Schurko A.M. & Logsdon J.M. 2008. An expanded inventory of conserved meiotic genes provides evidence for sex in *Trichomonas vaginalis*. *PLoS One* 3: e2879.

Maniatsi S., Baxevanis A.D., Kappas I., Deligiannidis P., Triantafyllidis A., Papakostas S., Bougiouklis D. & Abatzopoulos T.J. 2010. Is polyploidy a persevering accident or an adaptive evolutionary pattern? The case of the brine shrimp *Artemia*. *Mol. Phylogenet. Evol.* 58: 353–364.

Margulis L. & Sagan D. 1986. *Origins of sex.* Yale University Press Newhaven and London.

Mark Welch D. & Meselson M. 2000. Evidence for the evolution of bdelloid rotifers without sexual reproduction or genetic exchange. *Science* 387–388: 403–407.

Mark Welch J.L. & Meselson M. 1998. Karyotypes of bdelloid rotifers from three families. *Hydrobiologia* 387: 403–407.

Mavárez J.U.S. & Linares M. 2008. Homoploid hybrid speciation in animals. *Mol. Ecol.* 17: 4181–4185.

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

Meier R., Shiyang K., Vaidya G. & Ng P.K.L. 2006. DNA barcoding and taxonomy in Diptera: a tale of high intraspecific variability and low identification success. *Syst. Biol.* 55: 715–728.

Menken S.B.J. & Wiebosch–Steeman M. 1988. Clonal diversity, population structure, and dispersal in the parthenogenetic moth Ectoedemia argyropeza. *Entomol. Exp. Appl.* 49: 141–152.

M'Gonigle L.K. & Otto S.P. 2011. Ploidy and the evolution of parasitism. *Proc. R. Soc. Lond. B Biol. Sci.* 278: 2814–2822.

Muller H. 1964. The relation of recombination to mutational advance. *Mutat. Res–Fund. Mol.* 1: 2–9.

Neiman M. & Schwander T. 2011. Using parthenogenetic lineages to identify advantages of sex. *Evol. Biol.* 38: 115–123.

Otto S.P. & Whitton J. 2000. Polyploid Incidence and Evolution. *Annu. Rev. Genet.* 34: 401.

Paquin C. & Adams J. 1983. Frequency of fixation of adaptive mutations is higher in evolving diploid than haploid yeast populations. *Nature* 302: 495–500.

Parker Jr E.D. & Niklasson M. 2000. Genetic structure and evolution in parthenogenetic animals. In: Singh R.S. & Krimbas C.B. (eds.), Evolutionary genetics: from molecules to morphology, Cambridge University Press, Cambridge, pp. 456–474.

Peters A. & Lively C. 2007. Short-and long-term benefits and detriments to recombination under antagonistic coevolution. *J Evol Biol* 20: 1206–1217.

Pons J. 2006. DNA-based identification of preys from non-destructive, total DNA extractions of predators using arthropod universal primers. *Mol. Ecol. Notes* 6: 623–626.

Posada D. 2008. jModelTest: phylogenetic model averaging. *Mol. Biol. Evol.* 25: 1253–1256.

Posada D. & Crandall K.A. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

Pro Natura. 1997. *Psychidae Sackträger Schmetterlinge und ihre Lebensräume. Arten, Gefärdung, Schutz. Schweiz und Angrenzende gebieten Band 2 (ed. by Lepidopterologen–Arbeitsgruppe) pp. 165–308.* Pro Natura – Schweizerische Bund f¨ur Naturschutz, Basel, Switzerland.

Provencher L.M., Morse G.E., Weeks A.R. & Normark B.B. 2005. Parthenogenesis in the *Aspidiotus nerii* complex (Hemiptera: Diaspididae): a single origin of a worldwide, polyphagous lineage associated with *Cardinium* bacteria. *Ann. Entomol. Soc. Am.* 98: 629–635.

Rach J., DeSalle R., Sarkar I.N., Schierwater B. & Hadrys H. 2008. Character–based DNA barcoding allows discrimination of genera, species and populations in Odonata. *Proc. R Soc. Lond. B Biol. Sci.* 275: 237–247.

Ratnasingham S. & Hebert P.D.N. 2007. BOLD: The Barcode of Life Data System (http://www. barcodinglife. org). *Mol. Ecol. Notes* 7: 355–364.

Rhainds M. 2010. Female mating failures in insects. *Entomol. Exp. Appl.* 136: 211–226.

Rhainds M., Davis D.R. & Price P.W. 2009. Bionomics of Bagworms (Lepidoptera: Psychidae). *Annu. Rev. Entomol.* 54: 209–226.

Rhainds M., Gries G. & Min M. 1999. Size-and density-dependent reproductive success of bagworms, Metisa plana. *Entomol. Exp. Appl.* 91: 375–383.

Rice W.R. & Friberg U. 2009. A Graphical Approach to Lineage Selection Between Clonals and Sexuals. In: Schön I., Martens K. & van Dijk P. (eds.), Lost Sex. The Evolutionary Biology of Parthenogenesis. First ed., Springer Science + Business Media B.V, Dordrecht The Netherlands, pp. 75–97.

Richards A.J. 1997. *Plant breeding systems.* Stanley Thornes, Cheltenham, UK.

Roe A.D. & Sperling F.A.H. 2007. Patterns of evolution of mitochondrial cytochrome c oxidase I and II DNA and implications for DNA barcoding. *Mol. Phylogenet. Evol.* 44: 325–345.

Ronquist F., Huelsenbeck J.P. & van der Mark P. 2005. MrBayes 3.1 Manual. *School of Computer Science.Florida State University .*

Rozen, S., Skaletsky, H.J. 2000. Primer3 on the www for general users and for biologist programmers. In: Krawetz S, Misener S (eds) Bioinformatics methids and protocols: methods in molecular biology. Humana Press, Totowa, pp. 365–386. .

Rubinoff D. 2006. Utility of mitochondrial DNA barcodes in species conservation. *Conserv. Biol.* 20: 1026–1033.

Satler J.D., Starrett J., Hayashi C.Y. & Hedin M. 2011. Inferring species trees from gene trees in a radiation of California trapdoor spiders (Araneae, Antrodiaetidae, *Aliatypus*). *PloS one* 6: e25355.

Sauter W. 1956. Morphologie und Systematik schweizerischen *Solenobia*–arten. *Rev. Suisse Zool.* 63: 451–550.

Scali V. 2009. Metasexual stick insects: model pathways to losing sex and bringing it back. In: Schön I., Martens K. & van Dijk P. (eds.), Lost Sex. The Evolutionary Biology of Parthenogenesis. First ed., Springer Science + Business Media B.V., Dordrecht The Netherlands, pp. 317–345.

Schlupp I. & Tobler M. 2008. Expanding the horizon: the Red Queen and potential alternatives. *Can. J. Zool.* 86: 765–773.

Schön I., Martens K. & Halse S. 2010. Genetic diversity in Australian ancient asexual Vestalenula (Ostracoda, Darwinulidae): little variability down under. *Hydrobiologia* 641: 59–70.

Schurko A.M., Neiman M. & Logsdon Jr J.M. 2009. Signs of sex: what we know and how we know it. *Trends Ecol. Evol.* 24: 208–217.

Schwander T. & Crespi B.J. 2009. Multiple direct transitions from sexual reproduction to apomictic parthenogenesis in *Timema* stick insects. *Evolution* 63: 84–103.

Schwander T., Vuilleumier S., Dubman J. & Crespi B.J. 2010. Positive feedback in the transition from sexual reproduction to parthenogenesis. *Proc. R Soc. Lond. B Biol. Sci.* 277: 1435–1442.

Seiler J. 1961. Untersuchungen über die Entstehung der Parthenogenese bei *Solenobia triquetrella* FR (Lepidoptera, Psychidae). *Mol. Gen. Genet.* 92: 261–316.

Shinohara W., Ushio Y., Seo A., Nakato N., Kono M., Kudoh H., Tobe H. & Murakami N. 2010. Evidence for Hybrid Origin and Segmental Allopolyploidy in Eutetraploid and Aneutetraploid *Lepisorus thunbergianus* (Polypodiaceae). *Syst. Bot.* 35: 20–29.

Silvertown J. 2008. The evolutionary maintenance of sexual reproduction: evidence from the ecological distribution of asexual reproduction in clonal plants. *Int. J. Plant. Sci.* 169: 157–168.

Simon J.C., Delmotte F., Rispe C. & Crease T. 2003. Phylogenetic relationships between parthenogens and their sexual relatives: the possible routes to parthenogenesis in animals. *Biol. J. Linn. Soc.* 79: 151–163.

Simon C., Frati F., Beckenbach A., Crespi B., Liu H. & Flook P. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Ann. Entomol. Soc. Am.* 87: 651–701.

Song Y., Scheu S. & Drossel B. 2012. The ecological advantage of sexual reproduction in multicellular long-lived organisms. *J. Evol. Biol*.

Stenberg P. & Saura A. 2009. Cytology of Asexual Animals. In: Schön I., Martens K. & van Dijk P. (eds.), Lost Sex. The Evolutionary Biology of Parthenogenesis. First ed., Springer Science+Business Media, Dordrecht The Netherlands.

Stenberg P. & Lundmark M. 2004. Distribution, mechanisms and evolutionary significance of clonality and polyploidy in weevils. *Agricult. For Entomol.* 6: 259–266.

Strutzenberger P., Brehm G. & Fiedler K. 2011. DNA barcoding-based species delimitation increases species count of *Eois* (Geometridae) moths in a well-studied tropical mountain forest by up to 50%. *Insect Science* 18: 349–362.

Suomalainen E. 1980. The Solenobiinae species of Finland (Lepidoptera: Psychidae), with a description of a new species. *Insect Syst. Evol.* 11: 458–466.

Suomalainen E., Saura A. & Lokki J. 1987. *Cytology and evolution in parthenogenesis.* CRC Press, Boca Raton, FL, United States of America.

Tagg N., Innes D. & Doncaster C. 2005. Outcomes of reciprocal invasions between genetically diverse and genetically uniform populations of Daphnia obtusa (Kurz). *Oecologia* 143: 527–536.

Tamura K., Peterson D., Peterson N., Stecher G., Nei M. & Kumar S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol. Biol. Evol.* 28: 2731–2739.

Tobler M. & Schlupp I. 2008. Expanding the horizon: the Red Queen and potential alternatives. *Can. J. Zool.* 86: 765–773.

Tobler, M.& Schlupp, I. 2010. Differential susceptibility to food stress in neonates of sexual and asexual mollies (*Poecilia*, Poeciliidae). *Evol. Ecol.* 24: 39–47.

Tsutsui N., Suarez A., Spagna J. & Johnston J.S. 2008. The evolution of genome size in ants. *BMC Evol. Biol.* 8: 64.

Valentini A., Pompanon F. & Taberlet P. 2009. DNA barcoding for ecologists. *Trends Ecol. Evol*. 24: 110–117.

Van Doninck K., Schön I., De Bruyn L. & Martens K. 2002. A general purpose genotype in an ancient asexual. *Oecologia* 132: 205–212.

Van Valen L. 1973. A new evolutionary law. *Evol. Theor.* 1: 1–30.

Vandel A. 1928. La parthénogenese geographique. Contribution a l´étude biologique et cytologique de la parthénogenese naturelle. *Bull. biol. Fr. Belg.* 62: 164–182.

Vorburger C., Lancaster M. & Sunnucks P. 2003. Environmentally related patterns of reproductive modes in the aphid Myzus persicae and the predominance of two 'superclones' in Victoria, Australia. *Mol. Ecol.* 12: 3493–3504.

Vrijenhoek R.C. 1979. Factors affecting clonal diversity and coexistence. *Am. Zool.* 19: 787–797.

Vrijenhoek R. 1984. Ecological differentiation among clones: the frozen niche variation model. In: Wöhrmann, K., Loeschcke, V (ed.), Population biology and evolution, pp. 217ą231. Springer–Verlag, Berlin, Heidelberg, pp. 217–231.

Wahlberg N. & Wheat C.W. 2008. Genomic outposts serve the phylogenomic pioneers: designing novel nuclear markers for genomic DNA extractions of Lepidoptera. *Syst. Biol.* 57: 231–242.

Ward R., Hanner R. & Hebert P. 2009. The campaign to DNA barcode all fishes, FISH-BOL. *J. Fish. Biol.* 74: 329–356.

Weeks A.R. & Hoffmann A.A. 2008. Frequency–dependent selection maintains clonal diversity in an asexual organism. *Proc. Nat. Acad. Sci.* 105: 17872.

Weeks A.R., Marec F. & Breeuwer J.A.J. 2001. A mite species that consists entirely of haploid females. *Science* 292: 2479.

Weismann A. 1893. *The germ–plasm: a theory of heredity.* Scribner's.

White M. 1973. *Animal Cytology and Evolution.* Cambridge University Press, Cambridge, Cambridge, UK.

Williams G.C. 1975. *Sex and evolution.* Princeton Univ Pr. Yassin A., Markow T.A., Narechania A., O'Grady P.M. & DeSalle R. 2010. The genus *Drosophila* as a model for testing tree–and character–based methods of species identification using DNA barcoding. *Mol. Phylogenet. Evol.* 57: 509–517.

Zharkikh A. 1994. Estimation of evolutionary distances between nucleotide sequences. *J. Mol. Evol.* 39: 315–329.

Zibaee A., Sendi J.J., Alinia F. & Etebari K. 2008. A study on biochemical differences among five different groups of rice striped stem borer *Chilo suppressalis* Walker (Lepidoptera: Pyralidae). *Invertebrate Surviv. J.* 5: 20–29.

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