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Cover: Meadow filled with polyploid plants? Photo by M. König

Summary

Polyploidy, the state when an organism has more than two copies of each chromosome, has been known since the early 20th century. Polyploidy is very common amongst plants and is recognized as a strong force for speciation. Approximately 30-80% of all plants today are believed to have originated via polyploidization events. Historically, focus has been on the morphological differences between polyploidy levels, and very little has been done on the ecological effects caused by polyploidy. The few studies conducted show that polyploidization alters the interactions between the plant and surrounding pollinators, herbivores and gall makers in the community. These altered interactions seem to be important for the establishment and survival of new polyploidy levels. Therefore, polyploid systems give us the opportunity to investigate how plant-animal interactions affect speciation.

Sammanfattning

Polyploidi, fenomenet när en organism har mer än två kopior av varje kromosom, har varit känt sedan tidigt 1900-tal. Polyploidi är väldigt vanligt inom växtvärlden, ungefär 30-80% av alla nu levande arter tros ha bildats via polyplodisering. Historiskt sett har majoriteten av forskningen rörandes polyploidi fokuserats på att förstå de morfologiska skillnaderna olika polyplodinivåer, medan vi knappt vet något om vilka ekologiska effekterna en polyplodisering medför. De studier som har gjorts visar dock att polyplodiseringen påverkar samspelet mellan växten och omgivande pollinatörer, herbivorer samt gallbildande insekter i samhället. Dessa ändrade interaktioner verkar dessutom vara viktiga för etableringen och överlevnaden av nya polyplodinivåer. Därför ger polyploda system oss möjligheten att kunna studera hur växt-djurinteraktionerna påverkar artbildning.

Introduction

In ecology, numerous studies have been conducted to try to capture the effects of interacting species, and how these interactions shape the surrounding community (Herrera & Pellmyr 2002; Thompson 1994; Thompson 2005). Although polyploidy has been known for almost a century, there has been a surprisingly low interest in researching the ecological effects it might cause (Thompson 1999). Here I will review what polyploidy is, how it originates, and why it is important to consider polyploidy in a wider ecological perspective.

Polyploidy

Polyploidy is the state when an organism has more than two copies of each chromosome (Münzbergová 2006; Soltis et al. 2007). The term polyploidy was coined by Winkler (1916) and was later divided into two sub classes, autopolyploidy and allopolyploidy (Kihara & Ono 1926). An autopolyploid organism has originated from gene duplications within a species, and allopolyploidy is a gene duplication of a sterile hybrid which thereby becomes fertile. Polyploidization was early recognized as an important way for species to originate (Winge 1917). However, most polyploid cytotypes are not regarded as different species. Especially the autopolyploids, which are very similar to their original cytotypes phenotype, are often considered as one species. There is an ongoing argument on how these cytotypes should be handled in the nomenclature (see Soltis et al. 2007).

Polyploidy is very common in the plant community, as many as 30 to 80% of all flowering plants are thought to have originated from earlier polyploidization events (Soltis et al. 2007). Traditionally, allopolyploidy has been seen as more important, and only a handful of species were recognised as “true” autopolyploids (Grant 1981; Soltis et al. 2003). Recent studies, though, have proved that autopolyploidies are more common than previously thought (Soltis et al. 2003). Genomic studies has also shown that many diploid species today seems to have been polyploid, but mutations, gene-rearrangements, -deletions and -silencing has turned the species into functional diploids. Maize and *Arabidosis* are two examples of such species groups (Gaut et al. 2000; Vision et al. 2000). Genomic studies on non-plant organisms have shown that polyploidization has been an important evolutionary force there too. Yeast (Wolfe & Schields 1997), salmonids (Allendorf et al. 1984) and amphibians (Beçak & Beçak 1998)

are some examples of the animal groups that contain ancient polyploidization events. Polyploidy amongst mammals are very rare, but there are some known cases, such as the bush rat *Tympanoctomys barrerae* (Gallardo et al. 1999).

The polyploidization event per se is known to alter morphological characters in plants. The cells become enlarged as a consequence of the increased nuclear content (Levin 1983), which results in plants growing taller and developing enlarged plant parts, such as flowers and leaves. Polyploid plants flowers later with fewer flowers (Janz & Thompson 2002; Mabel 2004), and they often manage to tolerate harsher environments than their diploid ancestors (Ehrendorfer 1980). The ability to survive harsher environments is believed to be a result of the increased number of genes, giving the plant the possibility to become more heterozygotic and variable. This accounts especially for allopolyploid individuals, who should be able to benefit from genes from two species (Levin 1983).

The differences between cytotypes in morphology have been proven to alter plant-animal interactions. Enlarged flowers in combination with altered flowering period changes the interaction with pollinators (Husband & Schemske 2000). Changes in morphology and chemical substances may alter the herbivore's choice when it chooses between the two polyploidy levels (Levin 1983). The changes in habitats sometimes moves the newly formed polyploid into an enemy free space, but may also create stronger interactions with herbivores that only partly coexisted with the plant before the switch of habitat.

Establishment of new cytotypes

One of the major questions with polyploidy is how new cytotypes are established in the wild. Usually only a few polyploid organisms are produced at the time, and these are more likely to become fertilized by the original cytotype, which will result in sterile hybrids (Husband 2000). In simulations, the new cytotype is swamped by the pollen of the former more abundant cytotype, and few or none of the seeds develop into pure non-hybrid offspring of the new cytotype. This frequency dependent selection is known as minority cytotype exclusion (Levin 1975) and should either act as a quick selection for reproductive barriers, or failure to establish for the new cytotype. The reproductive barriers developed are usually a combination of: altered flowering phenology, divergence in the pollinator species visiting due to

morphological changes in flower characters, inhibiting the germination of pollen from the other cytotype or becoming self fertilising and thereby excluding the risk of getting swamped by the more common cytotype.

Many factors can interact to prevent hybridization between cytotype levels. The geographic distance, both on a micro- and macro scale, and changes in morphological and phenological characters affect the outcome of the plant-animal interactions. Post-mating barriers can also be developed to hinder hybridization in mixed populations. This makes it hard to pin point which characters that are a direct effect of the polyploidization and which are by-products of other events.

The fireweed, *Chamerion angustifolium*, is a perennial weed that can be found both in Europe and North America. Only diploids and tetraploids are known in North America. Through most of their range the cytotypes grows allopatric, with diploids growing at higher latitudes and altitudes than tetraploids (Mosquin 1966). However, there are some areas close to the Rocky Mountains where they grow in sympatry and yet seems to be almost completely reproductively isolated. The diploids flowers slightly earlier than the tetraploids, but there is still a large overlap in flowering time. There are small but distinct differences in flower morphology that bumblebees, their main pollinator, seem to be able to recognise (Husband & Schemske 2000). In these sympatric populations tetraploids are always less abundant than the diploids, but they attract more pollinators (Kennedy et al. 2006). There also seems to be some post-mating barrier amongst the tetraploids. The diploids produce more triploid than diploid offspring when pollinated with a mix of diploid and tetraploid pollen, tetraploids on the other hand produces only a handful of triploid offspring (Husband et al. 2002).

In other polyploidy plants, for example *Ranunculus adoneus* (Baack 2005), *Secale cereale* (Hagberg & Ellerström 1958) and *Dactylis glomerata* (Maceira et al. 1993) similar patterns of reduced seed production when growing sympatric with other cytotypes have been found. Self-pollination and spatial differencing seems to be the most important cues to prevent minority cytotype exclusion in these cases.

Changes in plant-herbivore interaction

Pollinators seem to be able to alter the probability of establishment as well as the forthcoming evolution of the new cytotypes. By solely responding to new plant characters, the interaction between the plant and pollinators will become altered, resulting in new selection pressures (Segraves & Thompson 1999). Herbivores also respond differently to different cytotypes due to changes in plant characters, e.g. enlarged plant size (Arvanitis et al. 2008) or higher levels of secondary compounds (Vestad 1960; Levin 1983). The interaction between the herbivore and the new cytotype can be either strengthened or weakened due to secondary effects of the polyploidization (Nuismer & Thompson 2001, Thompson et al. 2004). Changes in habitat preferences can move an otherwise attractable cytotype out of the herbivores habitat, thereby avoiding the interaction. In *Cardamine pratensis* the octoploid cytotype, which grow larger than the tetraploid, is preferred for ovipositioning by the butterfly *Anthocharis cardamines*. However, *A. cardamines* only oviposit in sunny meadows and fields while the octoploids prefer damper and more shaded habitats and thereby avoid the interaction (Arvanitis et al. 2007).

Gall makers need to be able to interact with the plants genome in order to induce and maintain the gall until the larva is fully developed. A polyploidization is equal to reformation of the genome and gall makers should be more or less efficient in taking control of the transcription in different cytotypes. Goldenrod (*Solidago altissima*) in North America occurs as diploid, tetraploid and hexaploid, and is galled by five species of gall wasps. All five species of gall wasps prefers one of the three cytotypes, and in some cases a gall wasp species may avoid one cytotype completely when a more preferred one grows sympatric (Halverson et al. 2008). It is also among the gall makers that the only known case of a completely new interaction between an herbivore and a higher polyploid level has been found. The gall midge *Dasinuera cardaminis* is not found in the tetraploid community of *Cardamine pratensis*. However, it is commonly found amongst the octoploids. *D. cardaminis* is also known to oviposit on the sister species *Cardamine amara* that partly coexist with both the octoploid and tetraploid. It seems like the polyploidization event altered the genome in a way that enabled *D. cardaminis* to expand its niche from *C. amara* to include octoploid *C. pratensis* (Arvanitis et al. 2010).

Polyploidy and speciation

Evolution has traditionally been thought to proceed slowly, where mutations assemble over eons of time (Darwin 1859). Today's biologist has learned the hard way that evolution under the right condition can precede at incredible high speed (Thompson 1998), as with antibiotic resistant bacteria and viruses like HIV (Steinhauer & Holland 1987; Palumbi 2001). It has been questioned whether speciation can occur under sympatric conditions. Although a couple of cases have been presented, e.g. cichlids in the Victorian lake (Schliewen & Klee 2004; Seehausen et al. 1997) and the apple- and hawthorn moths in North America (Feder & Filchak 1999), it's still debated whether they are actual cases of sympatric speciation or if the speciation occurred through isolation via some unknown barrier. Polyploidy is often seen as one of the few clear cases of sympatric speciation, due to its immediate effect on the whole genome (Soltis et al. 2007).

The close relationship between the cytotypes, the plant-animal interactions they share and the slight difference in habitat choices turns polyploid systems into good study system to investigate speciation and how the environment and animal interactions affects the outcome. As mentioned earlier, the close genetically relationship ought to lead to a competitive situation between the newly formed and the original cytotype. This should either lead to a rapid evolution for separated niches or the extinction of the newly formed cytotype. If a niche separation occurs, a patchwork of mono- and mixed populations will arise. In sympatric populations the interaction between the new cytotype and the insect community might affect the outcome of old interactions. Thereby polyploid systems give us the opportunity to investigate how environment and plant-animal interactions affects the outcome of speciation.

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