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Forum

Fire-mediated effects on polyploid biology

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Cold temperatures have been posited as a key driver of polyploidy (possession of multiple chromosome sets). However, high temperatures associated with fire, and the indirect impact of post-fire environments in polypoid formation and establishment deserve more attention for a comprehensive understanding of polyploid ecology, evolution, and current distributions.

Global polyploid distributions

Recent investigations into polyploid biogeography highlight an association between cold temperatures and polyploidy. The tundra and taiga are the most polyploid-rich biomes on Earth [1], and it is well known that cold can stimulate **unreduced gamete (UG) formation** (see Glossary) [2]. However, many tropical savanna grasslands and temperate shrublands also show high instances of polypoid species, despite rarely being exposed to extreme cold. We suggest here that the role of fire in polyploid plant ecology and evolution deserves attention and might further explain patterns of polyploid distribution.

Fire is a strong ecological filter and evolutionary force that occurs in almost every ecosystem on Earth. Fire creates immense, but episodic, stress for the organisms living in these environments while altering coexistence dynamics and nutrient availability. Fire-prone biomes may select for polyploids due to their ability to tolerate myriad stressors [3]. He and Lamont [4] suggested that fire and components may play a mutagenic role in plant evolution, and Linder *et al.* [5] suggested that high polyploidy rates may have contributed to grassland ecosystems expanding in the Miocene, but the links between fire regimes and polyploidy have not been clearly articulated.

Mechanisms by which fire might promote polyploidy

To understand the potential role of fire in polyploid biogeography, one needs to consider the ecological and evolutionary factors driving the formation, **establishment**, and **persistence** of polyploid individuals in a community (Figure 1).

Autopolyploid formation

Fire can increase UG formation and somatic chromosome doubling through increased temperature and chemical stresses. Diploid pollen formation increased by a factor of ten in maize, *Zea mays*, exposed to temperatures over 40°C [6]. Surface fire regimes, such as those that occur in many temperate and tropical grasslands, produce such soil temperatures (30–50°C) [7] and could disrupt meiosis while reproductive tissues are developing just below the soil surface. **Pyrolysis** releases organic and inorganic chemicals with mutagenic properties that directly affect UG formation and somatic doubling. Organic **polycyclic aromatic hydrocarbons (PAHs)** released in smoke, that is, acenaphthene, cause polyploidy due to spindle fiber aberrations. Inorganic heavy metals and radioactive metal/metalloid ions can also be released by fire and induce mutations [3].

Allopolyploid formation

Synchronized post-fire flowering is an important strategy in fire-prone environments globally [8], which can increase the chances of hybridization, and, therefore, **allopolyploidization**. Hybridization is especially prevalent in genera with generalist pollinators and may be further enhanced by fire-induced UG formation facilitating interploidy hybridization. Polyploid-rich groups like grasses [9] and some **geophytes** respond quickly to dry-season fires by **resprouting**, which facilitates interspecific hybridization.

Establishment

Polyploids generally have larger cells and require more phosphorus and nitrogen for cell growth, photosynthesis, and DNA synthesis [10]. Consequently, demand for soil nutrients presents an initial challenge that newly formed polyploids must overcome for successful establishment (Figure 1). Fire rapidly recycles nutrients from burned biomass back to the soil via both wet and dry deposition [11]. In the short term, this may increase available nitrogen and phosphorus in soils to boost polyploid growth at a key stage of establishment. Over longer timescales, however, fire-prone landscapes may become depleted of both nitrogen and phosphorus [9], which might reduce the competitive ability. Polyploidy is associated with rapid

Glossary

Allopolyploid: polyploids formed via hybridization, combination of two different genomes from individuals of different species.
Autopolyploid: polyploids formed without hybridization, combination of genomes from individuals within the same species.
Establishment: successful germination and growth of an individual.
Fire intensity: energy released per unit time.
Fire return period: how often organisms are exposed to fire.
Geophyte: seasonally growing plant with a subterranean (sometimes partially above ground) storage organ.
Minority cytotype exclusion: newly formed polyploids are subjected to frequency-dependent selection, often where the rare ploidy is at a mating disadvantage.
Persistence: survival of a polyploid lineage through time, over multiple generations.
Pyrome: global syndromes of fire regimes.
Pyrolysis: process where decomposition of materials occurs at elevated temperatures (e.g., fire).
Polycyclic aromatic hydrocarbons (PAHs): a class of organic compounds that are produced by combustion.
Resprouter: plant species that can survive fire by regenerating from subterranean tissue.
Unreduced gamete (UG) formation: production of diploid gametes instead of typical haploid gametes.

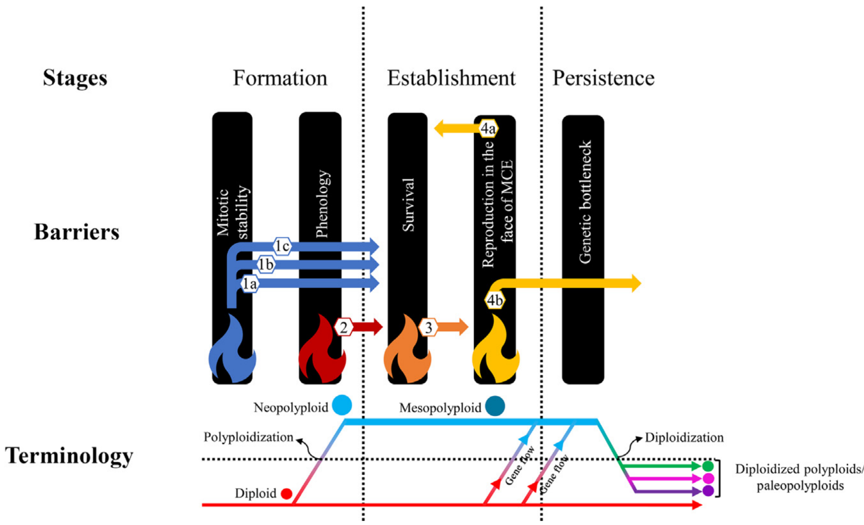

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Figure 1. Possible fire-mediated mechanisms that facilitate polyploid formation, establishment, and persistence. Heat (1a) polycyclic aromatic hydrocarbons (1b), and/or liberated heavy metals (1c) could all collectively or independently induce somatic chromosome doubling in seeds/seedlings or unreduced gamete formation in mature plants by altering meiotic and mitotic stability. Synchronized phenology following fire in prerain post-fire flowers and some grass species potentially facilitates allopolyploidization (2). Once formed, these neopolyploids can establish in habitats where nutrients are bolstered following fire, or in habitats that are opened by fire (3). In this establishment phase, recurrent fires provide multiple opportunities for polyploid formation and establishment and assist in overcoming minority cytotype exclusion (4a) and ensure genetic variation from recombining diploid relatives or from neopolyploids of unique origins sharing their genomes (4b) to overcome genetic bottlenecks and assortative mating.

growth rates and larger plants, which would assist establishment in highly competitive post-fire environments.

Persistence

Minority cytotype exclusion (MCE) is a key constraint for polyploid population-level persistence [12]: when polyploid formation depends on random mutations, it is rare for sufficient polyploid individuals to arise in a population at the same time to enable long-term persistence of the polyploid lineage. By providing a large-scale stochastic cue for formation and stablishment, fire could encourage synchronised polyploid formation, which helps to overcome a mating bottleneck. Further, any promotion of asexual reproduction would also reduce mating bottlenecks for neopolyploids. Resprouting, an important fire adaptation, ensures individual longevity and polyploid maintenance in the population. The large bud banks required for successful post-fire resprouting [13] also enable mutations to accumulate in the gene pool.

Fire regimes and fire adaptations likely to be associated with polyploidy

Fires vary globally, ranging from frequent grass-fueled fires occurring every 2–10 years, to rare, intense fires with return times up to 300 years that release orders of magnitude more heat [14]. Not all of the mechanisms identified above would be active in all environments where fires burn, and some fire regimes might prevent, instead of enable, polyploidy.

These mechanisms by which different fire regimes might affect polyploid ecology and evolution provide expectations for which environments, and which life forms, would be expected to show higher instances of polyploidy if fire was an important driver of their evolution and ecology (Box 1). Grass-dominated fire regimes, with their low-intensity surface fires, would be expected to have high polyploidy, providing soil surface temperatures known to promote UG formation and selecting for resprouting plants that can accumulate mutations and overcome MCE. Of such regimes, those with shorter **fire return periods** would also be expected to have higher instances of polyploidy. The highest fire return periods tend to occur in tropical grasslands/savannas (every 1–2 years) so if ploidy decreases with latitude within grasslands, instead of increasing as expected if cold temperatures were the main mechanism, then this might be evidence for fire as an important driver. Regions with low-intensity frequent fires are therefore the most obvious systems that would promote polyploidy (Box 1), but more intense, less frequent fires may release stored mutagenic compounds and create high-nutrient, competitor-free environments for new polyploids to establish. This would enable polyploid persistence, especially for the non-reseeding components of their flora.

The resprouting life history is more common in frequent, low-intensity fire regimes [12]. For grasses, geophytes, and woody plants, the bud banks at ground level will be exposed repeatedly to fire-related mutagenic agents, and MCE will also be a lower risk for these perennial resprouting plants. In contrast, serotinous plants that recover from seedbanks after fire become more common when fires are intense enough to kill the adults, and infrequent enough for individuals to accumulate a seedbank between fires. UG formation induced by fire is unlikely to occur in serotinous plants, as reproduction is complete when a fire returns and post-fire reproduction is impossible, leaving only the purportedly less common somatic chromosome doubling fire-induced pathway to polyploidy.

Box 1. Predictions for polyploid ecology and evolution in different pyromes

The **pyromes** (global fire regimes) identified in [14] provide a framework to predict polyploidy instances at global and local scales, or across ecoregions (Figure I). Here, we distill these down to different combinations of fire intensity and fire frequency. If the heat and chemicals released by the fire stimulate UG formation (**autopolyploidy**) and synchronized post-fire flowering stimulates hybridization (allopolyploidy), regions with more frequent fires (Figure IA) will have more opportunities for meiotic aberrations to occur, leading to higher fluxes of polyploids into the community, and consequently, a reduced chance of MCE. When high frequency is combined with a high intensity, there could be an increased propensity for polyploid formation, as these pyromes have the advantage of seldom causing soil to exceed 70°C due to limited time available for fuel accumulation [7]. Consequently, temperatures remain within ranges reported to promote UG formation. In systems with short return intervals (Figure IB), propensity for establishment is predicted to be increased by more formation events, and it is currently unclear whether frequently burning ecosystems provide the nutrient pulse to boost establishment and competitive advantages that may arise for polyploid. In systems with long return intervals, establishment is already decreased by fewer formation events, which makes overcoming MCE a greater challenge. When fires do return to these systems, they likely boost soil nutrients and can work in conjunction with the cold to foster establishment and persistence of polyploids (Figure IC). If the fire is too intense, formation, and subsequently establishment, is likely unattainable (*).

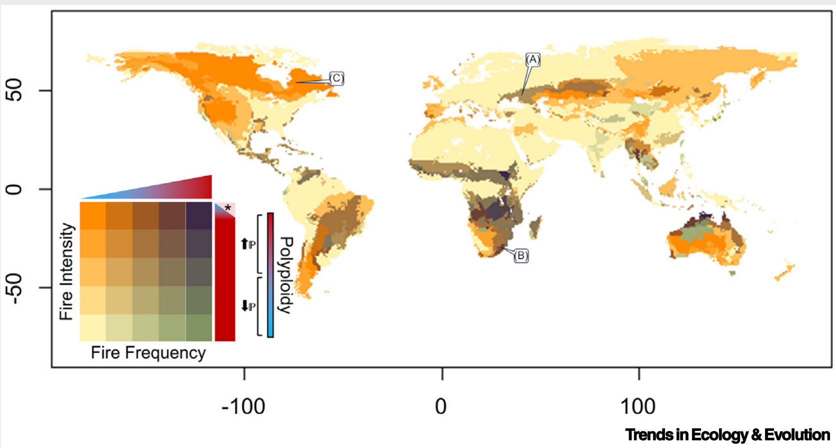

Figure I. Bivariate choropleth map of fire intensity versus fire frequency across ecoregions. Here, we indicate how intensity and frequency are predicted to relate to incidences of polyploidy. (A) The Pontic steppe (infrequent, cool fires); (B) the Drakensberg montane grasslands, woodlands, and forests (frequent, cool to intense fires); (C) the Eastern Canadian Shield taiga (rare, intense fires).

Cold and fire could also act in combination to drive polyploidy. Cold snaps [2] and heat and mutagenic chemicals [4] could stimulate UG formation, with fire additionally creating nutrient pulses and available niches to improve probabilities of polyploid persistence. Moreover, both cold and fire promote perennial resprouting life forms which would further enable successful establishment of polyploid individuals and promote coexistence with diploid progenitors (Figure 1). The expectation that cold, fire-prone places would have the highest instances of polyploidy is supported by data in [1], but exploring polyploidy presence within grasslands that vary in their exposure to cold and fire would help to test the relative importance and interactive effects of these two agents.

Polyploidy and the Pyrocene

As the Earth temperature rises, and fires become more frequent and more intense [15], this global future has the potential to shape plant diversification via polyploidization. Comparing polyploidization rates across clades that are in fire-prone or fire-poor landscapes may help further explain biogeographic patterns of polyploids. Experimental work testing the contribution of different aspects of fire and fire-related mechanisms (**fire intensity**, nutrient availability, rate of UG formation, life history traits) on polyploid formation and establishment is key to untangling the role of fire in polyploid ecology and evolution.

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Declaration of interests

No interests are declared.

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