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Global Change Biology: Museum Specimens Are More Than Meet the Eye

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Dead museum specimens are finding new life, providing critical data about otherwise hidden impacts of human-caused environmental change. New research powerfully leverages decades of plant collections to uncover global responses in floral pigmentation linked to ozone and climate change.

The ozone layer 15–30 km high in the Earth's stratosphere absorbs ultraviolet (UV) wavelengths of incoming radiation from the sun, thereby functioning as a protective filter against rays that cause harm to biological molecules and cells. Since the 1970s, emissions of human-made ozone-depleting substances have notoriously caused ozone layer reductions globally [1], which in turn has led to alarming increases in UV radiation reaching the Earth's surface [2]. International efforts played a monumental role in curbing this trend, but biologically damaging UV radiation remains high, and recovery is complicated by many factors, including climate change [3]. Despite their importance, biological responses to increased UV radiation is often overlooked relative to other global change factors. A seeming lack of historical baseline data required to accurately quantify long-term organismal trait changes is a major challenge. In this issue of *Current Biology*, Koski and colleagues [4] dig into the museum record to provide an innovative measure of pigmentation shifts in plant flower petals as a result of long-term ozone and temperature changes. Although these pigments may not be visible to the human eye, they hold big ecological and evolutionary importance.

Increased pigmentation is an adaptive response shared across animals and plants to protect against UV damage, though animals have received more attention with clear links to human skin cancer [5]. Considerably less is known

about ozone depletion effects on other organisms, especially plants. Flowering plants are widely admired for their diversity in flower petal colors and color patterns. But beyond our human perception in the visible light spectrum underlies secret floral patterns. Many flowers exhibit a UV 'bullseye' pattern formed by UV absorption towards the flower center and UV reflectance at the edges [6], primarily caused by flavonoid pigments.

What is the function of floral displays visible in the UV spectrum? Most notably, insect pollinators can perceive visual signals outside the human visible spectrum [7]. As such, the floral UV bullseye serves as a 'landing pad' to attract pollinators, guiding them to plant nectar. Perhaps just as important, UV patterns can also serve critical protective functions to reduce molecular damage to pollen, as well as heat regulation. Previous studies have demonstrated the role of these floral pigments within [6] and across [8] species. However, it is unknown if recent human-induced ozone depletion has affected UV pigmentation in plants.

To test whether human-caused changes in the ozone layer have altered UV-absorbing pigmentation patterns in plants, Koski and colleagues [4] directly measured flowers from 1,238 herbarium specimens collected from the 1940s to recent years (Figure 1). The researchers cleverly used UV photography to capture images of flowers collected before and during global ozone depletion. They found petal UV pigmentation has increased by roughly 2% per year globally. Changes in UV pigmentation were directly linked to stratospheric ozone levels at the time each specimen was collected, thereby linking increases in UV radiation resulting from this global change factor. This groundbreaking study is the first to document this long-term response.

Organisms are simultaneously experiencing many competing selection pressures in the current era of global change. Therefore, documenting and interpreting shifts in UV pigmentation in flowers are far from straightforward. Indeed, not all 42 species exhibited the same response over time, despite a general overarching average pattern. Individual species vary in many ways

Figure 1. Flowers on herbarium specimen.
Marsh marigold (*Caltha palustris*) specimen collected in 1979 in Pennsylvania, USA (CM344680; Kunsman 2998). As biological snapshots in time, herbarium specimens are being tapped in unexpected ways to understand biological change at scales otherwise not possible.

relevant to their predicted pigmentation response to UV stress, including evolutionary history (physiological constraints), habitat (exposed or shaded), and flower shape (pollen-producing anthers exposed or concealed by petals). For instance, the study authors predicted that species with concealed anthers should be less responsive to UV-driven shifts in UV floral patterns because their pollen was protected from UV rays. Yet surprisingly, even some species with concealed anthers showed increases over time in UV pigmentation in flowers. When statistically isolating the ozone effect, species with exposed anthers exhibited increased UV pigmentation with lower ozone levels at time of collection, while those with concealed anthers exhibited the opposite pattern. While their analysis accounts for evolutionary history, floral anatomy, and environmental context, the results generate not only many answers, but also many questions.

True for nearly every aspect of functional ecology, evolutionary and physiological tradeoffs exist, such that organismal performance is a balanced response to competing pressures.

Natural selection is not about global maximization, but rather, local optimization in light of competing pressures and evolutionary constraint [9]. In other words: it's complicated. For the case of UV floral pigmentation, variable selection pressures exist for thermoregulation (heating up of flowers is adaptive in cold environments, maladaptive in hot environments), photoprotection (reduces UV damage to pollen in exposed flowers, but at an unnecessary metabolic cost for concealed flowers or shaded environments), and pollinator attraction (co-evolved visual cues for efficient reproduction in outcrossing species).

Due to multiple, sometimes competing, selection pressures in a rapidly changing world, shifts in UV floral pigmentation are more than simple responses to ozone depletion alone. Climate, especially temperature patterns [5], plays a key role in the biological function of pigmentation. Pairing both ozone and temperature data with each specimen, Koski and colleagues [4] were able to start to disentangle the complex web of combined and separate effects

of climate and ozone responses. Their results highlight the importance of considering interacting global change factors. They found species with concealed anthers responded to long-term temperature trends, while those with exposed anthers responded more strongly to long-term ozone trends. These results have significant ecological implications, with potential for ozone and climate change to lead to contrasting evolutionary trajectories across the plant kingdom.

This novel herbarium-based study provides new compelling evidence that floral pigmentation has rapidly shifted over the past century of global environmental change, but the underlying mechanisms and impacts of these plant responses are left partly to speculation. Past research indicates that floral UV trait expression can be strongly heritable [10], supporting the notion that these recent changes could be genetic (adaption). However, trait plasticity (acclimation) cannot be ruled out. Further, the metabolic cost of UV production is unknown, as is the related fitness benefits for altered UV under ozone depletion. Given the context-dependent benefits and tradeoffs across thermoregulation, photoprotection, and pollinator attraction, it is likely that species could be negatively impacted by mismatched responses to climate and ozone over time. Of the 42 species analyzed, over half did not show a positive change over time in UV pigmentation. Species that unexpectedly did not alter floral pigmentation or shifted in an expected direction may be driven by other factors or evolutionary constraints limiting species-level responses. These varied responses across species suggest impacts may manifest beyond individual species to community function more broadly. Pollinator preferences presumably remain similar under ozone depletion, suggesting disruptions in co-evolved plant–pollinator interactions and plant performance.

Collected by many tens of thousands of botanists over the past three centuries, the 392+ million plant specimens in 3,300+ herbaria collectively document the world's plant diversity through time [11]. First collected primarily for taxonomic purposes, herbarium specimens are

increasingly being used in unanticipated ways to provide biological discoveries scarcely imagined by plant collectors and museum curators just decades ago [12]. The use of specimens as data sources to document biological responses to global change has been profound in recent years [13], especially in regards to shifts in plant phenology [14] but also in phenotypic and genotypic change more broadly [15]. This study by Koski and colleagues [4] is not only pioneering for its novel findings but also for its innovative use of museum specimens. Few studies have used specimens to look for hidden UV floral pigmentation patterns across species [8,16]. Only one study exists in relation to ozone-driven shifts in flavonoids in an Antarctic moss species [17] and another on leaf hair trait responses to elevated UV irradiance [18]. Empowered by widespread museum digitization [19] and efforts to connect disparate data [20], it is an exciting new era for collections that must be fostered by continued collecting and specimen use [12,15,19]. Koski and colleagues [4] confirm that each specimen has important stories to tell, but we have to listen (or in this case, look). What other discoveries are hidden in plain sight in museum collections?

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