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Conservation Matters: Contributions from the Conservation Committee

Anthropogenic threats to high-altitude parnassian diversity

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Introduction

Global mean annual temperatures increased by $\sim 0.85^\circ\text{C}$ between 1880 and 2012 and are likely to rise by an additional 1°C to 4°C by 2100 (Stocker *et al.* 2013). Anthropogenic climate warming is driving the geographic distributions of most species toward higher latitudes and elevations (Parmesan 2006). Climate-driven local extinctions are already widespread, and recent results show that such extirpations have occurred in hundreds of species, including 47% of 976 plant, insect, vertebrate and marine invertebrate species surveyed (Wiens 2016).

For insects, numerous studies have shown the impact of climate and habitat change. Perhaps the most alarming recent one was on flying insect diversity, with collecting traps deployed over 27 years in 63 nature protection areas in Germany (Hallman *et al.* 2017). They found a seasonal decline of 76% and mid-summer decline of 82% in flying insect biomass due to unknown large-scale changes whose influence extended into protected areas. Climate change has more clearly been implicated in both latitudinal and elevational shifts in Lepidoptera species distributions. A pioneering study on 35 non-migratory European butterflies showed that 63% of the species shifted their ranges to the north by 35–240 km in the 1900's, and only 3% shifted to the south (Parmesan *et al.* 1999). Such range shifts carry risk; a recent study of Canadian butterflies has demonstrated significant "climate debt," with an increased gap between required and realized range shifts for species with smaller ranges (Lewthwaite *et al.* 2018). In the tropics, a study of geometrid moths at Mount Kinabalu, Malaysia, found that in 42 years the leading margins of their distributions shifted uphill faster than the trailing margins retreated, with many species increasing their elevational

extents (Chen *et al.* 2011). However, this did not result in increases in range area because the area of land available declines with increasing elevation. Accordingly, extinction risk may increase long before species reach a summit, even when undisturbed habitats are available. This is a particular concern for high-altitude adapted insects, like the parnassians or Apollo butterflies (genus *Parnassius*).

Current diversity and evolution of parnassians

Parnassians are well-known butterflies representing at least 60 species with a northern circumpolar and mountain distribution. They occur in almost all mountain ranges of the Northern Hemisphere from the Rocky Mountains to the Himalayas. Except for a few widespread species like *Parnassius apollo* (Fig. 1), most current *Parnassius* diversity is restricted to mountain valleys or the highest places of the world, with many microendemic species. High-altitude species often live at 4000m, occurring even at Everest Base Camp (e.g. *Parnassius epaphus*).

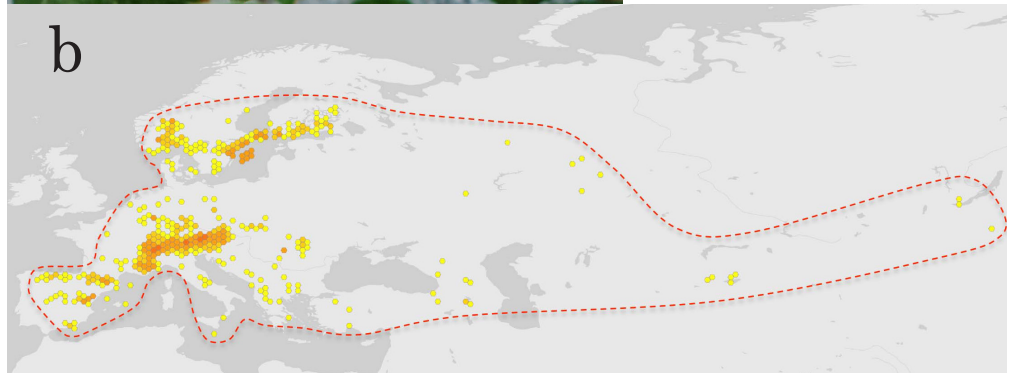
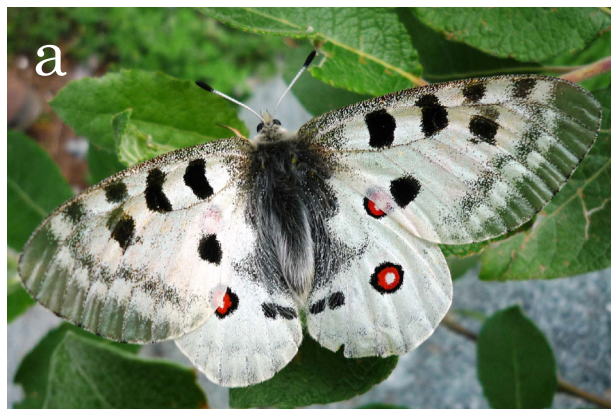


Figure 1. The Mountain Apollo (*Parnassius apollo*) is a key species for understanding the impact of climate change on extinction risk. a) Live butterfly in Southern French Alps (Mercantour National Park around 1000 m). Photo by Fabien Condamine. **b)** The distribution of *P. apollo* from Southern Spain to East Central Asia (Kyrgyzstan) mapped using 15,534 georeferenced observation records in GBIF (<https://www.gbif.org/species/1938810>).

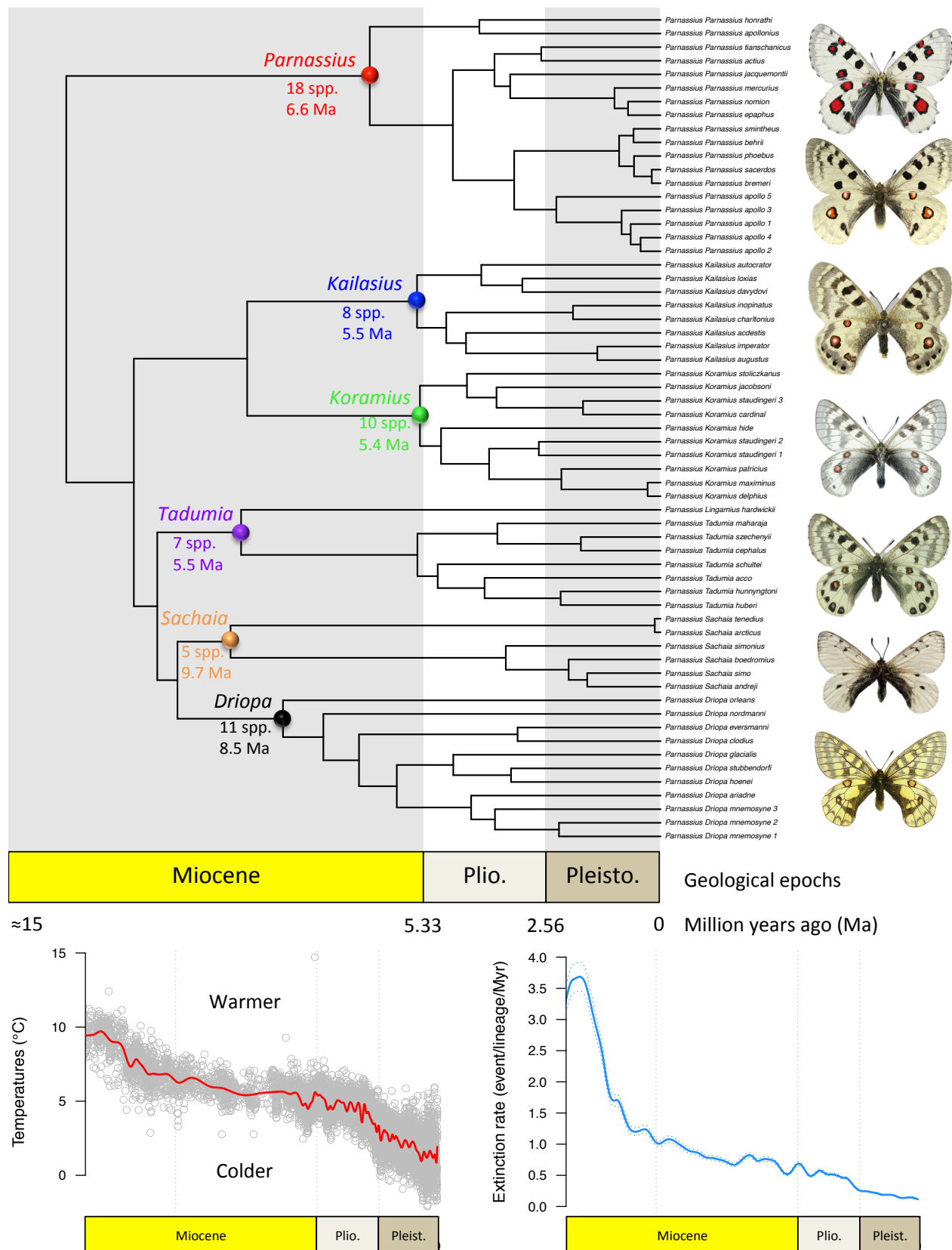


Figure 2. The evolutionary history of *Parnassius* indicates the genus originated 15 million years ago in Central Asian mountains. The phylogeny is based on both molecular and morphological data (adapted from Condamine *et al.* 2018). The dated phylogeny allows its biogeographic history to be inferred from current distributions, and the diversification rates to be estimated. In this case, we inferred a peak in extinction rates linked to the warmest time in the Miocene.

A comprehensive revised parnassian phylogeny indicates a mid-Miocene origin in Central Asian mountains and the Tibetan Plateau (Fig. 2, Condamine *et al.* 2018). Our data suggest that parnassians colonized mountains during a warming event 15 Ma which suggests that *Parnassius* was already a mountain-adapted group that escaped warm climate of this period. The genus subsequently diversified into six subgenera that constitute independent mountain radiations. Some subgenera are isolated mountain radiations in a local area (e.g. subgenera *Kailasius* and *Tadumia* in the Himalayas), while others colonized multiple mountain areas (e.g. subgenera *Driopa* and *Parnassius*). Although allopatric speciation has been an important mechanism in the diversification of *Parnassius*, a diversity equilibrium has been reached and sympatric overlap between species is now common within subgenera, suggesting ecological constraints on the creation of new species (Condamine 2018).

Many *Parnassius* species are isolated in mountain patches and at high risk of extinction from environmental change (Todisco *et al.* 2010, 2012; Fig. 3). As mountain specialists they can likely track their climatic niches by climbing up mountains until they can go no higher (Wilson *et al.* 2005; Settele *et al.* 2008). Given that a substantial part of their current species diversity already occurs at high altitude, parnassians are especially likely to be threatened by climate change. Using a phylogeny of parnassians, diversification models indicate that they have been historically sensitive to global warming, with their extinction rate increasing with warmer temperatures (Fig. 2). Projecting

this evolutionary trend to future climate implies that parnassian species will have a high probability of going extinct as the world becomes warmer, and a cascade effect can be expected when their ecological interactions get reshuffled with host-plant species dropping out.

Status and threats to parnassian diversity

Parnassians are conspicuous mountain insects that are both attractive to collectors and easy to monitor as adults. Decreased population sizes can be detected and allow assessment of extinction risk for species. Based on numerous studies, four major anthropogenic threats to *Parnassius* species can be identified (Fig. 4).

First, global climate change will directly affect species distributions, with the elevational distribution of *Parnassius* species shifting upward on mountains. However, mountain ranges are finite geographical and ecological areas with constraints on movement, and even the highest mountains constitute ecological and evolutionary limits for parnassians (Condamine 2018). There is evidence for an upshift of 200m for the distribution of *Parnassius apollo* in central Spain (Wilson *et al.* 2005). Multiple studies on the Rocky Mountain parnassian (*Parnassius smintheus*) based on two decades of observations and experimental data show the effect of climate change on overwintering survival, larval development, date of emergence and adult activity, with both low and high extreme temperatures in November causing the most population change (Roland and Mat-

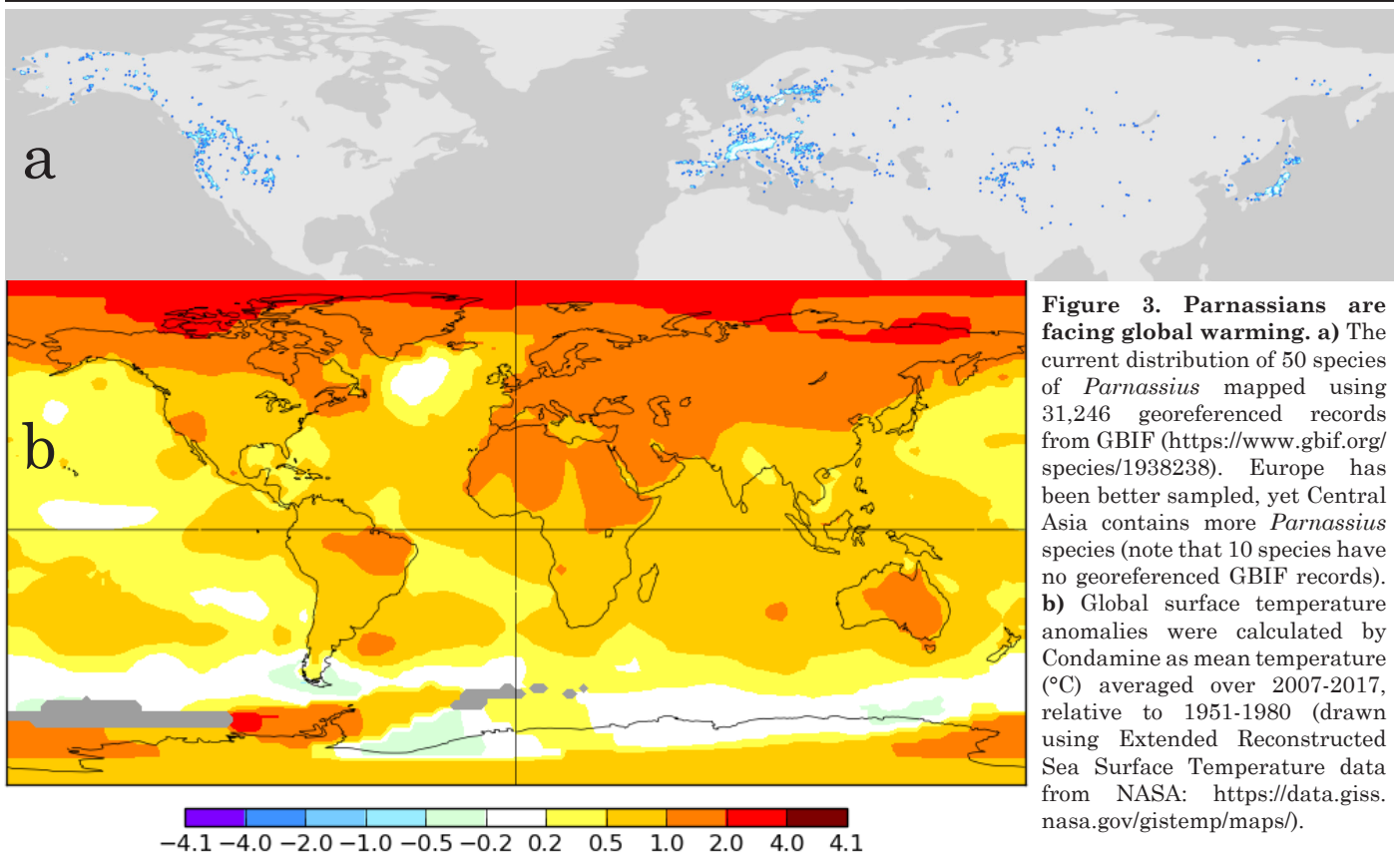


Figure 3. Parnassians are facing global warming. a) The current distribution of 50 species of *Parnassius* mapped using 31,246 georeferenced records from GBIF (<https://www.gbif.org/species/1938238>). Europe has been better sampled, yet Central Asia contains more *Parnassius* species (note that 10 species have no georeferenced GBIF records). **b)** Global surface temperature anomalies were calculated by Condamine as mean temperature (°C) averaged over 2007-2017, relative to 1951-1980 (drawn using Extended Reconstructed Sea Surface Temperature data from NASA: <https://data.giss.nasa.gov/gistemp/maps/>).

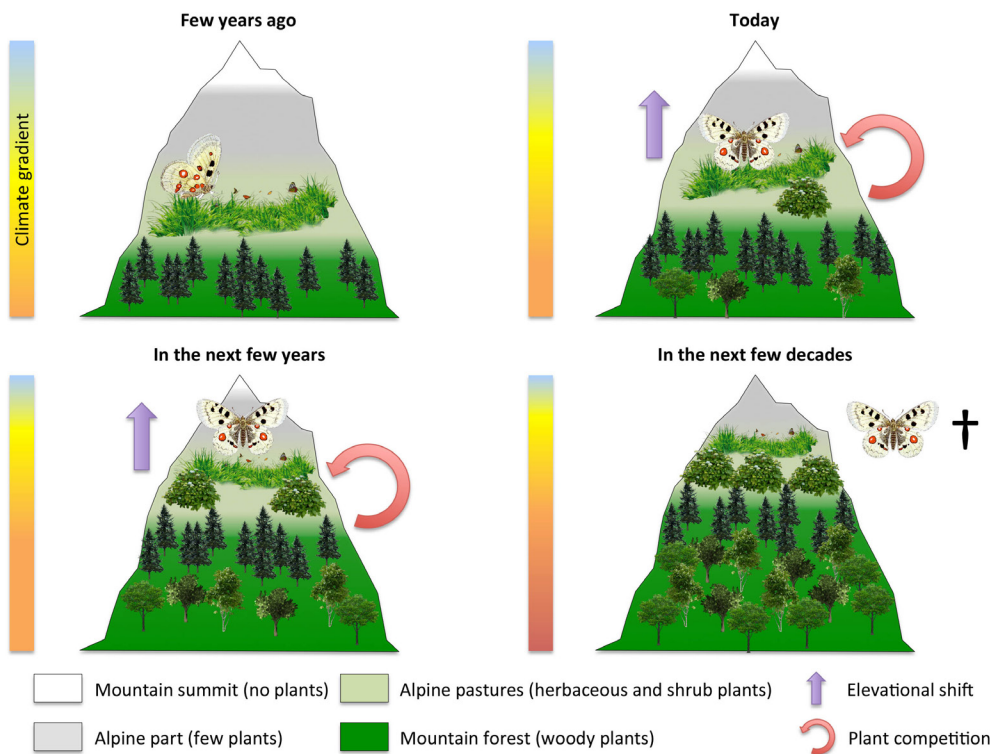


Figure 4. Schematic of current threats on Parnassius. Combined abiotic and biotic factors affect *Parnassius* survival, and climate warming induces elevational shifts for both *Parnassius* and vegetation (purple arrow). Reshuffling of vegetation initiates novel biotic interactions with host plants potentially becoming less available to the butterflies (red arrow). The combination of climate warming and vegetation change also leads to a drastic size reduction of living area for both *Parnassius* and their host plants, which are caught between mountain summits and colonization barriers of unsuitable ecological conditions, eventually leading to butterfly extinction.

ter 2016). Much *Parnassius* species diversity is located in areas where climate warming has been the most severe (+2°C in average over the last 10 years, Fig. 3), leading to an increased extinction risk for high-elevation Parnassians.

Second, global climate change is leading to shifts in vegetation habitat structure and the biotic interactions of *Parnassius* host plants. Plant species are massively and rapidly moving toward mountain summits, with the rate of increase in plant species richness accelerating on European mountain summits and strikingly synchronized with accelerated global warming (Steinbauer *et al.* 2018). This is reshuffling plant communities and changing biotic interactions between insects and plants. A groundbreaking study in the European Alps argues that accounting for novel competitive interactions may be essential to predicting species' responses to climate change accurately (Alexander *et al.* 2015). They show that species range dynamics depend not only on their ability to track climate, but also the migration of their competitors and the extent to which novel and current competitors exert differing effects (i.e. asymmetry in the importance of changing competitor identity at leading versus trailing range edges).

Third, high-mountain pastures can be damaged by cattle and other livestock. A recent study documents the impact of cattle grazing on butterflies in Tien Shan, a vast

mountainous territory in Central Asia. This region contains a substantial proportion of all *Parnassius* species, and 13 of the 17 species are endemic (Condamine *et al.* 2018). Korb (2015) shows evidence that two high-altitude species, *Parnassius delphius* feeding on *Corydalis* and *Parnassius actius* feeding on *Rhodiola*, are declining over time because of grazing pressures. Korb reported that areas with *Corydalis* and *Rhodiola* were reduced by at least half between 1999 and 2008. Although cattle do not eat these *Parnassius* food plants, many plants were trampled and overwintering plant parts suffered hoof damage.

Finally, over-collecting may threaten Parnassians. Demand for specimens is clear. For example, on April 22, 2018, on eBay we found that *Parnassius* had higher numbers of specimens for sale than any other swallowtail genera except *Papilio*: 644 entries for *Parnassius*, 1051 for the 200 species of *Papilio*, and 332 for the 100 species of *Graphium*. This only means that *Parnassius* are prized by collectors, and it does not by itself demonstrate an effect due to collecting. Such collecting is hard to document, although Sperling has anecdotally noticed a precipitous decline over 20 years in a population of *Parnassius evermannii* on Pink Mountain (British Columbia), which has been subjected to substantial collecting pressures with little obvious change in the composition of vegetation on this mountaintop.

Parnassius apollo, with all its subspecies endemic to mountain areas distributed throughout the Palearctic (Fig. 1, Nakonieczny *et al.* 2007), may provide an analog for other *Parnassius* species. Since the first half of the twentieth century, *P. apollo* populations have declined and became rare or extinct in several European countries (Collins and Morris 1985; Descimon *et al.* 2006; Nakonieczny *et al.* 2007). The main causes for this decline seem to be anthropic, such as shepherding, pollution, tourism, collecting or habitat loss (Nakonieczny *et al.* 2007). Other causes for the decline could be related to the fact that the species is very sensitive to habitat alteration and climate change. *Parnassius apollo* populations are particularly small and isolated in the south of Europe, where their distribution is restricted to mountain ranges (Todisco *et al.* 2010). In Spain, each of the 23 described subspecies of *P. apollo* is endemic to a different mountain range. Historical data

indicates that the altitudinal range of essentially all Spanish subspecies of *P. apollo* has been moving upslope in response to climate change, resulting in smaller and more isolated populations (Wilson *et al.* 2005).

Although some collectors have made efforts to possess every subspecies and population, the impacts of collecting on the observed declines are less clear. Nonetheless, over-collecting is considered to have contributed to the rarity of this species today in Finland, Italy, and Spain (Collins and Morris 1985), and *Parnassius apollo* was the first invertebrate to be listed in CITES and IUCN lists as a vulnerable species (IUCN 2018). It is also listed in the European Red Data Book as a species with a high climate change risk (Settele *et al.* 2008). Accordingly, laws exist in many countries to restrict collecting, and to monitor imports and exports of specimens. However, these laws may also discourage monitoring of populations by amateurs, reducing understanding of local population dynamics and the amount of occurrence data that can be used to inform conservation actions. Further, these laws do not address the main threats, which are climate change and habitat alteration.

Protecting the environment will help to safeguard species

A growing number and variety of anthropogenic threats affect all parnassians worldwide. Many parnassian species and subspecies will disappear in this century if no action is taken. We respectfully suggest that the following measures, whether by scientists, educators, or concerned citizens, would have the largest positive impact:

1. Parnassians are among the largest and most charismatic mountain butterflies, and are easy to recognize in their habitat. There are numerous monitoring studies on *Parnassius apollo* but fewer on other *Parnassius* species. We need a broader view of the status of populations of other species, including the effect of climatic changes and other anthropic factors on the extinction risks of *Parnassius*, particularly in Central Asia.
2. Parnassians show high intra-specific variability due to disjunct distributions in isolated habitats (valleys, mountain summits). Better species delimitations would ultimately support clearer understanding of what to protect.
3. Parnassians are excellent indicator species of the overall condition of ecosystems and for monitoring the environmental quality of endangered biotopes. They also serve umbrella species for protecting a wide range of co-existing species in the same habitats. Active measures to protect high-altitude meadows in *Parnassius* ecosystems, including limiting grazing by cattle and other ungulates, would greatly help them to cope with climate change.
4. Parnassians are widely-recognized symbols of endangered montane invertebrates, akin to what pandas represent for vertebrates. Their size, beauty, and familiarity

make them excellent candidates as flagship taxa for communicating conservation concerns and engaging the public. Parnassians are particularly useful in education, turning students' attention to the small living creatures that deserve protection. This is an opportunity for educators to play a disproportionate role in forestalling the extinction of these appealing creatures.

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