# Seasonal camouflage as a model to understand the scope for rapid adaptation in a changing world

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# Abstract

Human-driven environmental change is reshaping ecosystems and challenging species' ability to adapt. Understanding how genetic variation enables adaptation is crucial for conservation and requires exemplary systems to test hypotheses and make predictions. One particularly suitable model for studying climate-driven adaptation is seasonal color change (SCC), a phenological trait in which individuals transition between summer-dark and winter-white pelage/plumage to maintain camouflage. This review evaluates SCC as a model for predicting adaptive responses to climate change. First, we address the vulnerability of phenological traits to climate change, due to their dependence on photoperiodic cues and complex molecular regulation. Second, we review SCC literature across all 21 SCC species, summarizing knowledge on its regulation, the fitness costs of mismatch induced by snow loss, and the limited role of plasticity in buffering these effects. Third, we review recent findings on the genetic basis of SCC polymorphism that have linked adaptation to selection on pigmentation alleles with multiple evolutionary origins (including introgression and *de novo* mutations). Finally, we discuss the implications of the genetic architecture of SCC polymorphism for evolutionary rescue and conservation strategies, as well as methods for testing adaptation conditions using modeling approaches. While past research on SCC already showcased how predictive evolution can be incorporated into conservation action, we identify research gaps, including limited fitness data, taxonomic biases, and the need for real-time ecological and genomic monitoring. Addressing these gaps will improve the accuracy of predictive models and the success of management strategies aiming at protecting species' resilience to rapid environmental change.

# Keywords

seasonal color change; seasonal coat color polymorphism; climate change adaptation; adaptation genomics; conservation genomics

# Introduction

Rapid anthropogenic changes are causing escalating habitat losses, posing severe threats to species' survival by disrupting local environmental adaptations [1]. The current pace of species loss suggests that Earth is nearing mass extinction thresholds [2]. Understanding the impact of climate change on biodiversity and forecasting the potential for rapid adaptation is, therefore, one of the most critical and pressing challenges of modern science [3,4]. Such studies have often been conducted at the ecological level, assessing and monitoring changes in species communities [5,6]. Still, the adaptive potential of each species depends first and foremost on existing standing genetic variation, which provides a pool of variants upon which selection can act, fueling resilience to environmental change and diseases, and thus facilitating adaptation [4,7]. Neutral genetic diversity is a long-established metric for assessing the health of natural populations, their adaptive potential, and conservation status (e.g., by the International Union for Conservation of Nature, IUCN) [7]. Yet, genomic data also offer a powerful way to detect and quantify adaptive genetic variation, which can be incorporated into assessments of population status and predictions of adaptation to climate change [8]. Despite this potential, the knowledge of the genetic basis of adaptation is still seldom incorporated into conservation actions [9].

Traits with clear effects on fitness and predictable responses to environmental change serve as powerful models to understand the conditions under which adaptation to anthropogenic change can be expected [10]. Among these, seasonal, or phenological, traits enable organisms to maintain fitness year-round by synchronizing key life cycle events with seasonal environmental changes [11,12]. When the primary cue triggering phenological change remains fixed (for example, photoperiod), but environmental conditions change, a phenological mismatch occurs, which can affect individual fitness and the species' future survival [10,13].

Here, we synthesize seasonal color change (SCC) as a model adaptive trait to investigate genotype-to-phenotype-to-environment relationships underlying the scope for adaptation to climate change. SCC is a seasonal transition between summer dark and winter-white coats or plumages occurring in at least 21 species of mammals and birds across the Northern Hemisphere [13,14]. We connect phenological timing, bases of trait expression, costs of phenological mismatch, genetic architecture and evolution of winter color polymorphism, and prediction frameworks for future rapid evolutionary change, showing that SCC can serve as an especially suited model trait to gain both practical and general insights to foster the maintenance of biodiversity in a changing climate.

# Seasonally Flexible Traits

Habitats worldwide undergo seasonal environmental cycles, which tend to be more pronounced in temperate mid-latitude regions [15]. In response, diverse taxa have independently evolved mechanisms to cope with these seasonal fluctuations, including seasonal reproduction [16], hibernation [17], migration [18], molt [19], and others [11]. Although seasonal traits may share developmental pathways and expression patterns [20,21], specific physiological and molecular foundations of phenological traits can vary according to evolutionary and ecological contexts. These phenological traits require physiological adjustments across multiple biological levels [21], including molecular (e.g., gene expression [22,23]), cellular (e.g., proliferation [24,25]), metabolic (e.g., energy balance [26]), and hormonal (e.g., melatonin regulation [27]). Such adjustments reflect seasonal phenotypic flexibility — the ability of an organism to undergo reversible change in physiology or behavior in response to environmental changes [28].

Seasonal changes in phenotype are regulated by deeply conserved biological pathways across traits and taxa, with differences reflecting fine-scale adaptations to local ecological conditions [29]. For instance, conserved genetic pathways [30] and/or epigenetic mechanisms [31] have been shown to regulate several seasonal phenotypes. In particular, genes underlying circannual clocks, which are sensitive to seasonal light cycles, exhibit a regular pattern of expression in different cell types. This rhythmic expression coordinates downstream physiological pathways involving melatonin and prolactin hormones (discussed below), which further initiate various seasonal transitions [27,32-36]. Other hormones, such as gonadotropins, also influence seasonality, regulating reproduction, molt, and other physiological processes [13,37]. Overall, neuroendocrine regulation is usually functionally integrated and conserved across taxa [20,29].

Due to the existence of these conserved regulatory pathways, mutations affecting upstream regulatory components of seasonal phenotypes may have widespread pleiotropic consequences [38,39]. Such constraints may select for modularity or limit adaptive changes to the downstream portions of regulatory cascades, buffering against mismatches in other traits (for more details, see Box 1). Alternatively, selection on interconnected regulatory mechanisms could help coordinate multiple seasonal traits, ensuring that annual phenotypic transitions align with environmental pressures [38] (Box 1). For instance, this type of coordinated regulation is evident in organisms that undergo seasonal color change, where hormonal and genetic pathways govern the timing and extent of pelage or plumage color transitions in response to shifting seasonal conditions.

### BOX 1. THE INTEGRATION OF PHENOLOGICAL TRAIT REGULATION: A BUFFER OR A VULNERABILITY FOR CLIMATE CHANGE ADAPTATION?

The regulation of phenological traits is often interconnected, leading to overlapping genetic and physiological pathways, which can lead to pleiotropic effects [40]. This interdependence can enhance adaptation by synchronizing multiple traits [41], but it can also create vulnerabilities by limiting the ability for independent adjustments [39]. This limitation, known as the "cost of complexity" or "cost of pleiotropy", indicates that when one locus affects multiple traits, the rate of adaptation is often slower [42,43]. As climate change reshapes seasonal environments at an unprecedented pace [44-46], understanding the regulatory architecture of these traits and how their interactions influence adaptation becomes increasingly critical.

The degree of regulatory interconnection varies among different mechanisms. Upstream mechanisms play a critical role in regulating multiple seasonal traits. These include master genes (e.g., clock genes), transcription factors (e.g., THR1), and master hormones (e.g., melatonin) [47-49]. These elements act as central regulators, synchronizing various traits in response to environmental cues. While this coordination can be adaptive, it also creates constraints. Tightly linked traits might lead to ecological mismatches if an adaptive shift in one trait misaligns with changes in others [39]. For instance, if the timing of seasonal breeding changes but migration does not, species may face challenges in finding suitable habitats or mates. In contrast, downstream trait regulation usually involves other cis-regulatory elements that fine-tune gene expression in specific tissues or developmental stages. This results in *divergent pathways*, allowing traits to be regulated differently [50-52]. Additionally, genetic modularity can affect more pleiotropic pathways through *divergent regulation*, which allows for specific genetic control depending on the developmental stage, tissue, or environmental cue [53]. This flexibility allows for the independent evolution of traits such as seasonal migration, breeding patterns, and coat color.

Overall, changes in upstream phenological regulation may face greater challenges for adjusting phenotypes to rapidly shifting climates. In contrast, *divergent pathways* leading to downstream regulation of phenological traits may enhance species' adaptability by preventing disruptions across multiple traits. Furthermore, *divergent regulation* might help alleviate pleiotropy constraints through genetic modularity. This indicates that the adaptive pathways for coping with climate change are more likely to occur downstream and/or with a high level of genetic modularity.

## Seasonal color change

Seasonal color change (SCC) is a phenological trait characterized by molt transitions from a dark, typically brown, thinner coat (or plumage) in summer to a thicker white coat in winter [13]. This adaptive mechanism ensures year-round camouflage in environments with seasonal snow and is present in at least 21 species of mammals and birds (Fig. 1). Photoperiod is the primary trigger for molting in birds and mammals, including species that undergo SCC [48,54]. Molt phenology can also be influenced by intrinsic factors such as sex [37,55], age [37], body mass [37,56], and health condition [13,37], as well as extrinsic factors like temperature [57,58] and snow cover duration [59,60]. However, as snow duration decreases under climate change [61], phenotypic plasticity alone may not suffice to maintain effective camouflage, and evolutionary responses may be required to avoid fitness costs [57,62].

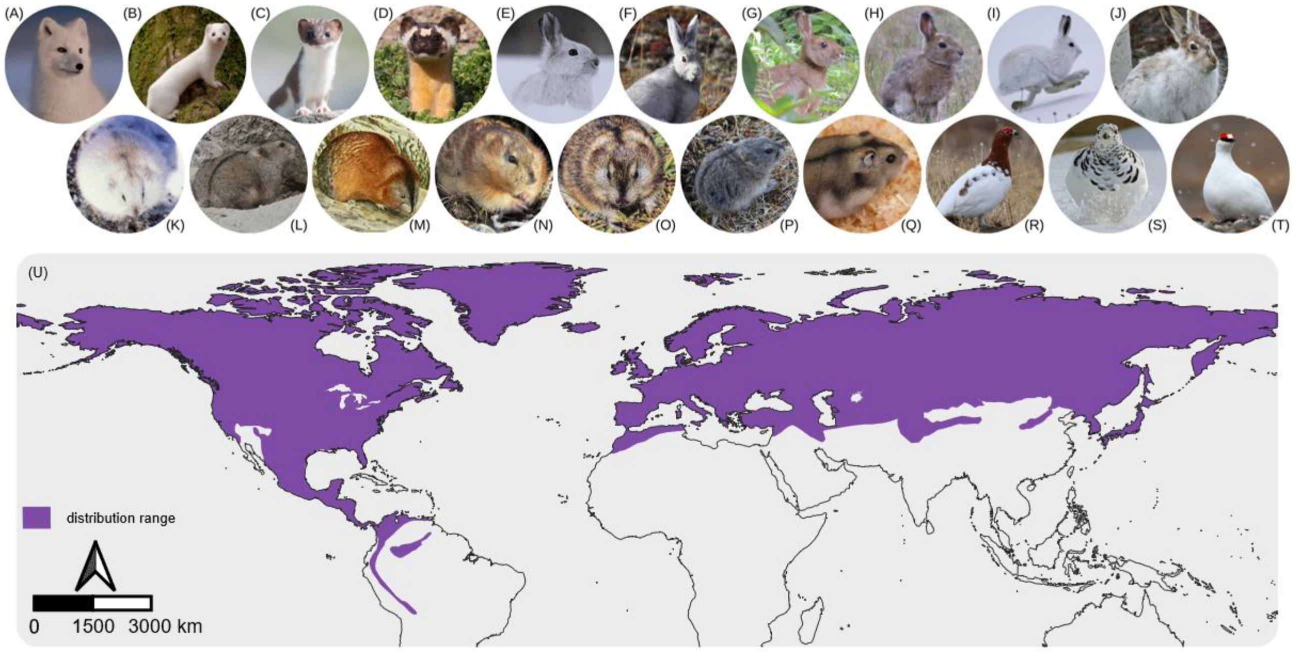


Fig. 1 | Cumulative geographic distributions of all 21 SCC species. Mammals - Canidae: (A) Vulpes lagopus (Arctic fox), Mustelidae: (B) Mustela nivalis (Least weasel), (C) M. erminea (Stoat), (D) Neogale frenata (Long-tailed weasel), Leporidae: (E) Lepus americanus (Snowshoe hare), (F) L. arcticus (Arctic hare), (G) L. brachyurus (Japanese hare), (H) L. othus (Alaskan hare), (I) L. timidus (Mountain hare), (J) L. townsendii (White-tailed jackrabbit), Cricetidae: (K) Dicrostonyx groenlandicus (Nearctic collared lemming), (L) D. hudsonius (Ungava collared lemming), (M) D. nelson (Nelson's collared lemming), (N) D. richardsoni (Richardson's collared lemming), (O) D. torquatus (Arctic lemming), (P) D. vinogradovi (Northern collared lemming), (Q) Phodopus sungorus (Winter-white dwarf hamster). Birds - Tetraonidae: (R) Lagopus lagopus (Willow Ptarmigan), (S) L. leucurus (White-tailed ptarmigan), (T) L. muta (Rock ptarmigan). (U) The combined distribution of the 21 species in purple, based on IUCN. Pictures rights: (A) Phil Chaon, (B) Karol Zub (C) Jing-Yi Lu, (D) Tom Benson, (E) Cam Nikkel, (F) Andrew Simon, (G) Rei Akiyama, (H) Alex Patia, (I) Claudio Spadin, (J) N Bertrand, (K) Mark C Long, (L) Fabrice Simon, (N) Justin Benjamin, (O) Frank Kienast, (P) Игорь Поспелов, (Q) Philipp Salzgeber, (R) Igor Dvurekov, (S) Nigel Voaden, (T) Ryan Shaw. Illustration rights: (M) National Geographic. A properly identified picture of the Cricetidae species Dicrostonyx nunatakensis is not available.

## The cost of color mismatch

Seasonal color molts allow species to track seasonal snow, enabling year-round camouflage [13]. The disruption of camouflage through phenotypic mismatch against the background has, with few exceptions [63,64], been shown to impact individual survival, potentially leading to local extinctions or population declines in species such as rock ptarmigan, willow ptarmigan, and snowshoe and mountain hares [57,65-70]. In snowshoe hares, camouflage mismatch has been shown to cause up to 7% decrease in individual weekly survival [70]. Variation in snow cover duration in both spring and fall molts also affects survival rates of willow ptarmigans, but the rate changes with age and sex [71]. In least weasels and snowshoe hares, studies using artificial models have recorded higher rates of predator attacks when body color mismatched the background [72-74], with white-on-brown mismatches facing greater predation rates than brown-on-white, indicating stronger selection against mismatches more likely to be induced by climate change [74].

Reductions in snow cover depth, extent, and duration across the Northern Hemisphere have been extensively documented [46,61,75], with further decreases projected under many climate change scenarios [46,57]. The combination of declining snow cover duration, due to anthropogenic climate change, and an unaltered photoperiod challenges the adaptive value of seasonal brown-to-white molts [57]. Projections of current color molt phenology against decreasing snow cover duration suggest increasing color mismatch in the absence of adaptive shifts, leading to range contractions and population declines [57,67,70,76]. Understanding the physiological mechanisms underlying seasonal color change is crucial for identifying adaptive pathways that may mitigate mismatch.

## Regulation of seasonal color change

Adaptation to shifts in snow seasonality could potentially evolve through physiological adjustments in the developmental timeline that controls molt and color change. Seasonal molts are regulated hormonally by signals that influence intracellular cascades and genetic regulatory mechanisms [77,78], which coordinate the expression of key pigmentation, molting, and circadian rhythm-related genes [13,22,23]. The process starts with the perception of photoperiodic changes, which, in mammals, occurs through photosensitive retinal ganglion cells that transmit light information to internal circadian pacemakers in the brain (the suprachiasmatic nucleus). In turn, in birds, other photoreceptor cells exist that allow direct photoperiodic change independent of the eyes [48,54]. The photoperiodic shift signal is transmitted through the suprachiasmatic nucleus to the pineal gland in the brain, which regulates melatonin production [79]. Melatonin is secreted in response to darkness and thus production increases with longer nights, further regulating prolactin production: high melatonin levels signal the pituitary gland to inhibit prolactin production, while low melatonin levels result in prolactin secretion [80,81]. These hormonal signals act upstream of genetic pathways regulating molt and pigmentation. While prolactin and melatonin have been shown to affect pigment production experimentally [27,34], the mechanism connecting the melatonin–prolactin axis to melanin synthesis remains unclear, whether through direct expression mechanisms (e.g., melatonin receptors in melanocytes) or via indirect pathways.

## BOX 2. MOLECULAR REGULATION OF SEASONAL COLOR CHANGE

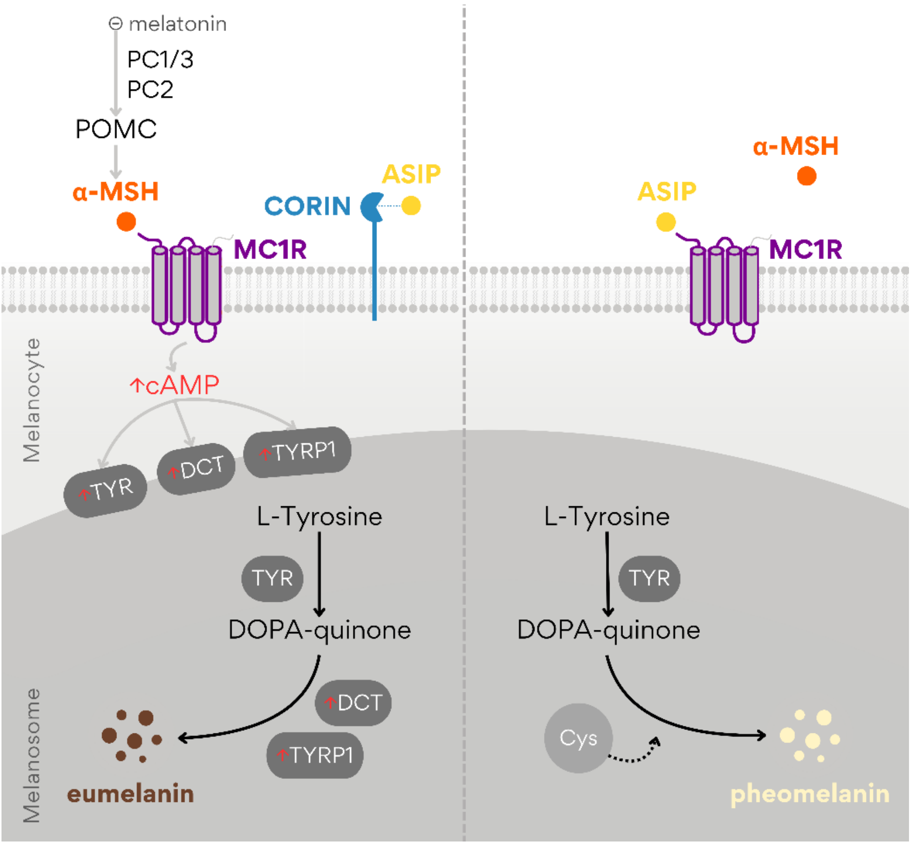


Fig. 2 | Pigmentation pathway in melanocytes and melanosomes. The illustration depicts the melanogenesis pathway, starting from POMC expression in keratinocytes (not shown), detailing the process within melanocytes, and including the contrasting binding effects of two molecules to MC1R in the melanocyte membrane – the agonist α-MSH (eumelanin production) and the antagonist ASIP (pheomelanin production). The simplified signaling cascade inside the melanosome highlights key enzymes that convert intermediate structures into the two types of melanin.

The pigmentation pathway primarily regulates the downstream pathway of seasonal color (Fig. 2). The production of eumelanin (dark melanin pigment) in melanocytes is promoted by the α-melanocyte-stimulating hormone (α-MSH), a peptide hormone derived from the cleavage of the pro-opiomelanocortin protein (POMC). When α-MSH binds to the melanocortin-1 receptor (MC1R) on the melanocyte membrane, it acts as an agonist, initiating a signaling cascade that increases intracellular cyclic adenosine monophosphate (cAMP) levels [82,83]. This boost in cAMP enhances tyrosinase activity and promotes the proliferation of other melanogenic enzymes (e.g., DCT and TYRP1), ultimately resulting in the synthesis of eumelanin [83,84]. Like prolactin, α-MSH is secreted when daylight is abundant and suppressed in low light conditions, being indirectly regulated by photoperiod [34,84]. However, it remains unclear whether this suppression is directly linked to melatonin release. Research suggests that melatonin does not inhibit α-MSH secretion but rather suppresses the melanogenic action of α-MSH by interfering with the accumulation of new tyrosinase molecules [85]. Furthermore, melatonin may affect the melanocortin system by reducing POMC expression, which hampers the binding of α-MSH to MC1R, leading to the production of lighter pigment instead [86].

The agouti signaling protein (ASIP) contributes to the production of lighter pigment, as ASIP acts as an antagonist to α-MSH at the MC1R receptor. When ASIP binds to MC1R, it decreases the activity of tyrosinase and inhibits the enzymes necessary for eumelanin production, leading to the synthesis of pheomelanin (light melanin pigment) instead [83,84]. Notably, in the presence of the transmembrane serine protease CORIN, ASIP does not bind to MC1R [87,88] The connection between ASIP and photoperiodic changes, and how ASIP production is regulated throughout the year to control seasonal color change, remains unknown. However, evidence suggests that ASIP expression level varies throughout the year, and between winter-brown and winter-white morphs [13,22].

The final step in the regulatory cascade within melanocytes is the transfer of melanin to keratinocytes, where it contributes to the formation of keratin structures, producing the colored coat/plumage during the hair/feather growth cycle [84,89].

Beyond hormonal regulation, existing literature on the genetic regulation of SCC molt shows a dynamic control of gene expression in response to seasonal cues [22,90]. Although the development of seasonal pelage molts is linked to the hair growth cycle and circadian clock genes, changes in the expression of key pigmentation genes are likely to shape seasonal transitions in color (for details on the downstream pigmentation pathway, see Box 2). For example, genes associated with melanogenesis have been found to be differentially expressed during the late fall molt in Arctic foxes [91]. Additionally, the expression of the *Agouti Signaling Protein* (*ASIP*), which is involved in the production of pheomelanin (light melanin pigment), is upregulated during the development of white fur coats in hare species [92,93]. Similarly, the *Tyrosinase-Related Protein 1* (*TYRP1*), which is linked to eumelanin (dark melanin pigment) production, is upregulated during the development of brown plumage in ptarmigan species [94]. These examples suggest that the color changes observed in many SCC species are likely related to regulatory mechanisms affecting gene expression. However, since the activation of these molecular pathways is likely tightly coupled with photoperiodic signals, the capacity of species with SCC to respond to other environmental cues may be constrained [13].

## Plasticity in SCC species

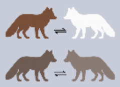
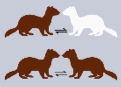
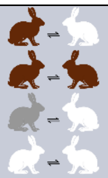
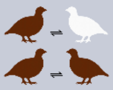
Although photoperiod is the primary trigger for SCC, the impacts of declining snow cover duration could be mitigated by plasticity in the timing or rate of color molts, or by behavioral adjustments [95]. However, responses to variation in temperature and snow cover duration across species appear insufficient to fully buffer against increasing camouflage mismatches [57,59,96-99]. For example, while there is some evidence for environmentally driven phenological variation of spring molts [57,59,96,98,99], fall molts show much less evidence for phenotypic plasticity [57,59,96,99]. Translocation experiments also suggest that molting plasticity rarely allows individuals to forgo the winter-white morph completely [37,65,100,101] (but see King and Powell [37], page 63).  Collectively, these findings imply strong genetic or physiological constraints on molt timing and expression, which may limit the potential for rapid adaptation to snow cover reductions in SCC species.

Likewise, there is limited and inconsistent evidence that behavioral plasticity provides an alternative means of mitigating climate change-induced mismatches. For example, mismatched hares do not appear to adjust their resting, hiding, or fleeing behaviors [59,102], but may show enhanced predator vigilance [103]. Conversely, ptarmigans appear to adjust their feeding strategies [104], select more cryptic resting spots, and may even soil white plumage when mismatched [105]. However, these behavioral changes occur in lekking systems where sexual selection on plumage color likely intensifies mismatch relative to other systems [105,106]. Given limited meaningful plasticity in coat color timing and behavior, evolutionary processes appear essential to foster future adaptation.

# Winter color polymorphism

The most substantial evidence for adaptation in SCC is the repeated evolution of winter color polymorphism in response to local variation in snow cover duration. As a result, most SCC species display geographic variation in the color of winter molts (white and brown morphs), resulting in color polymorphisms across species ranges [14] (Table 1). This trait polymorphism has been shown to have a genetic basis in many species, supported by common garden and translocation experiments [65,100], and direct genetic mapping of color variation [92,93,107,108]. The frequency of different winter color morphs varies geographically and is strongly correlated with snow cover duration and ephemerality [14], showing that the phenotypic clines are maintained by local adaptation for camouflage. For example, winter-brown morphs are more common in coastal and southern areas, where winter snow cover duration is low, absent, or highly variable. These findings suggest that genetic variation underlying alternative winter coloration morphs may be critical to fuel adaptive responses to global changes in snow cover duration [92,93,107]. There are also SCC species displaying summer color polymorphism (Table 1), but it is not the scope of this study to review this polymorphism.

**Table 1 | The spectrum of seasonal color change and winter color polymorphism**. Summary of key findings from studies on SCC species, organized by families. The graphical representation illustrates coat/plumage color phenotypes, with summer morphs on the left and winter morphs on the right. Below each graphical representation, the type of coat/plumage color polymorphism for the species is indicated, with winter polymorphisms highlighted in bold. The table synthesizes research on: (i) Seasonal color change, namely color descriptions, and (ii) Winter color polymorphism, including its genetic architecture (i.e., genetic basis and causative mutations), as well as its evolutionary origins, allele history, and type of selection detected locally. For information on specific species and references, please refer to the Supporting Material.

| | | <br>Foxes (Canidae) | <br>Weasels (Mustelidae) | <br>Hares (Leporidae) | <br>Hamsters/Lemmings (Cricetidae) | <br>Ptarmigans (Tetraonidae) |
|---|---|---|---|---|---|---|
| | | polymorphic in **winter** and summer | polymorphic in **winter** | polymorphic in **winter** or summer | not polymorphic | polymorphic in **winter** |
| Seasonal color change | Summer color: | brown or bluish brown | Brown | brown, gray, or white | brown | brown |
| | Winter color: | white or bluish brown | brown, white, or piebald | brown, white, gray, or continuous color (brown to white) | white | brown, white, or intermediate |
| | Color transition type: | binary | Binary | binary or continuous | binary | binary or continuous |
| Winter color polymorphism | Genetic Basis: | *MC1R* | *MC1R* | *ASIP, EDNRB, CORIN* | unknown | unknown |
| | Causative mutations: | Amino acid substitutions | Amino acid substitutions or INDELS | Nucleotide substitutions or INDELS | unknown | unknown |
| | Allele Origin: | expected *de novo* mutations | *de novo* mutations | ancestral variation, introgression | unknown | unknown |

| | | | | | |
|---|---|---|---|---|---|
| Evolutionary Pattern Across Species: | unknown | convergent evolution | standing adaptive variation, convergent evolution | unknown | unknown |
| Selection type for winter-brown morph: | unknown | positive, balancing | positive, balancing | unknown | unknown |

## The genetic basis of winter color polymorphism

Genomic studies focused across phenotypic transition zones (i.e., polymorphic populations where different winter color morphs coexist [14]) have consistently shown that genome-wide genetic variation is structured by geography and not by color morph [92,93,107,108], indicating that color variation responds to selective pressures irrespective of population structure. Whole genome scans of association [92,93,107-110] or candidate gene approaches [111] have identified genes of large effect underlying winter color polymorphism in lagomorphs and carnivores.

In hares, winter color polymorphism is manifested by both discrete and continuous variation (Table 1). In snowshoe and mountain hares, discrete trait variation has been linked to cis-regulatory changes influencing the expression of *ASIP* [92,93,109,112], with simple Mendelian inheritance of dominant winter-white and recessive winter-brown/gray variants [92,93]. In white-tailed jackrabbits, continuous brown-to-white winter color variation has been associated with at least three genes [*ASIP*, *Corin Serine Peptidase* (*CORIN*), and *Endothelin Receptor B* (*EDRNB*)] [107], with additive or epistatic contributions to the phenotype. In carnivores, protein-coding variation in the *Melanocortin 1 Receptor* (*MC1R*) gene has been shown to determine discrete winter color polymorphism in the Arctic fox [111,113], least weasel [108], and long-tailed weasel [110] (Table 1), with simple Mendelian inheritance with dominant winter-brown variants [108,110,111]. The alternative patterns of winter-brown recessive inheritance associated with *ASIP* and dominant inheritance associated with *MC1R* agree with the molecular functions of these genes and inheritance patterns found for light and dark color phenotypes across vertebrate taxa [51].

Overall, the studies conducted so far demonstrate that the melanin pigmentation pathway is strongly involved in determining winter color variation, either through regulatory or protein-coding changes (for details on the molecular regulation of the pigmentation pathway, see Box 2). Yet, the specific genes and genetic variants underlying the polymorphism vary across species [92,93,107-111] and even within species [109,110,112]. However, information on the genetic basis of winter color polymorphisms is still missing for many taxa. Advances in long-read sequencing and structural-variant detection have the potential to further resolve the genomic architecture of SCC polymorphism [114], particularly in systems with more complex coloration dynamics such as stoats and ptarmigans (Sup. Table 1) [37,115].

## Evolution of winter color polymorphism

Studies on winter color polymorphism across SCC species have also shed light on the evolutionary processes underlying the origin and persistence of the adaptive color variation within and across species. While the evolutionary origin of such polymorphisms remains elusive across most systems, available data show that the evolution of winter color variation has often been generated through repeated parallel evolution of re-derived brown winter morphs (for a discussion on re-derived vs. relic winter brown morphs, see Box 3). For example, in snowshoe and mountain hares, the origin of *ASIP* alleles causing gray winter morphs has been traced back to introgression from non-seasonally changing species (black-tailed jackrabbit and Iberian hare, respectively [92,93,116]). Similarly, winter-brown *ASIP* alleles contributing to continuous winter color variation in white-tailed jackrabbits have also introgressed from the black-tailed jackrabbit. Meanwhile, winter-brown variants in *CORIN* and *EDNRB* appear to result from the maintenance of ancestral genetic variation across species [107], pointing to a relic ancestral origin (Box 3). In weasels, different *MC1R* alleles have been shown to cause winter-brown phenotypes in distinct species [108,110], suggesting parallel adaptive evolution at the same gene, and a *de novo* origin of winter-brown alleles has been confirmed for least weasel populations in Europe [117] (Table 1). In the Arctic fox, genotyping of the *MC1R* region across Canidae did not reveal the occurrence of the Arctic fox candidate mutations in other species [111,118,119], which could point to a *de novo* origin.

### BOX 3. ANCESTRAL OR RE-DERIVED? THE EVOLUTIONARY PUZZLE OF WINTER-BROWN MORPHS AND THE REVERSIBILITY OF TRAITS UNDER UNSTABLE ENVIRONMENTS

The rarity of seasonal color change across mammals and birds suggests that winter whitening is a derived phenotype, as it occurs in only a few genera compared with the many taxa that remain brown year-round [13,14]. In this context, the ability to molt into a winter-white pelage/plumage can be considered a derived trait within each lineage where it occurs and, broadly, the winter-brown phenotype as an ancestral state.

Two main hypotheses can explain the origin of winter color polymorphism in SCC species: 1) The relic hypothesis suggests that winter-brown populations may represent remnants of the ancestral non-whitening condition, reflecting the long-term maintenance of ancestral variation. For example, in least weasels, some winter-brown populations have been hypothesized to be ancestral relics rather than re-derived morphs, although direct genetic evidence is lacking [120,121]; 2) Alternatively, the re-derivation hypothesis proposes that brown morphs have arisen secondarily through repeated losses of the whitening capacity. Most population genomic studies across multiple SCC species tend to support this view, showing that winter-brown morphs often result from geographically localized evolution disrupting SCC regulatory pathways, through hybridization or *de novo* mutations [92,93,107,109]. Yet, these hypotheses are not mutually exclusive. In white-tailed jackrabbits, a combination of ancestral polymorphism and recent introgression underlies winter-brown variation, suggesting that a combination of the phenomena may have been at play. In least weasels, the northern and central European winter-brown populations are re-derived from a *de novo* mutation [108,117], while the southernmost European populations may possibly be a relic [121]. These examples show that complex adaptive traits may persist, be lost, regained, or modulated in response to selective pressures. Repeated re-derivation of winter-brown morphs may also reflect post-glacial dynamics, where species or populations that evolved winter whitening subsequently lost it as climate and snow cover duration fluctuated towards the Holocene [122].

The persistence of winter-brown or -white alleles across the range of species with SCC is thus driven by a combination of selective mechanisms operating across heterogeneous environments (Table 1). Long-term balancing selection acting on ancient alleles has been suggested [107,117], alongside geographically localized signatures of positive directional selection favoring winter-brown phenotypes in some parts of population ranges, often in transition zones [92,93,108,117]. This combination of signatures illustrates how spatially varying selection can simultaneously maintain ancestral variation and drive locally adaptive divergence [123,124]. These dynamics likely stem from geographic variation in snow cover duration, which imposes contrasting selective pressures on coat color phenotypes by altering the fitness costs of seasonal camouflage mismatch. Such historical evolutionary dynamics that maintained adaptive polymorphisms may also shape the potential for future adaptation. Understanding the genetic architecture and selective landscape of winter color polymorphism is thus essential for predicting the scope for camouflage adaptation under climate change scenarios.

# Predictive frameworks for conservation

SCC species are facing severe habitat changes due to climate-driven decreases in snow duration (see section "The cost of color mismatch"), which is threatening population viability [14,70]. The persistence of these species under climate change depends on their capacity for evolutionary rescue, which could depend on their ability to recover or maintain positive population growth through rapid adaptive shifts in coat color in response to declining snow cover [14,125]. While environmental pressures define the direction of selection, it is the underlying genetic potential that determines whether adaptation can occur swiftly enough to prevent extinction [125]. Therefore, predicting the potential for evolutionary rescue in SCC species requires understanding the genetic architecture, selective dynamics, and spatial distribution of adaptive alleles underlying SCC variation.

## The scope for evolutionary rescue

The genetic architecture of SCC traits determines both the pace and trajectory of adaptation, which depend on key factors such as the number of loci, allelic relationships (dominance, additivity, epistasis), effect sizes, and linkage disequilibrium (LD) among loci [107,116,126-128]. For example, in many SCC species, winter coat color is controlled by a single large-effect locus [92,93,108,110,111]. In these cases, the dominance relationships of adaptive alleles strongly influence evolutionary responses to climate change. Recessive winter-brown alleles, as in hares [92,93], may persist as hidden standing variation that initially responds slowly to selection because heterozygotes remain winter-white [116]. Conversely, dominant winter-brown alleles, such as those in least and long-tailed weasels [108,110], are immediately exposed to selection and can spread rapidly when reduced snow cover favors brown morphs [129]. In the white-tailed jackrabbit, on the other hand, winter color polymorphism has a multigenic and largely additive genetic basis, resulting in more continuous winter color variation, which leads to more rapid adaptive responses and lower extinction risk in simulated populations confronted with reduced snow cover duration [107]. A multigenic architecture resulting in continuous variation may enable more gradual phenotypic shifts, allowing intermediate forms to track progressive environmental change. Additive inheritance can accelerate adaptive responses by acting on multiple loci simultaneously [130,131], with the magnitude of each contribution depending on effect size [132], whereas epistasis and LD among loci may either facilitate or constrain evolution depending on the direction of selection [133,134].

The underlying evolutionary mechanisms generating adaptive genetic variation determine how such variation translates into population persistence. Adaptation can rely on either standing genetic variation or *de novo* mutations, each with distinct implications for the speed and predictability of evolutionary change [4,125,126]. In hares, winter-brown morphs arose from ancestral or introgressed alleles maintained at low frequencies, which may enable rapid evolutionary rescue as snow duration declines [92,107,109,112,116,135]. In contrast, carnivores, such as weasels, evolved winter-brown phenotypes through independent mutations, suggesting a slower initial response but greater potential for parallel adaptation across lineages [110,111,117,119,135]. Population size, connectivity, and selection intensity may further shape these dynamics: small or isolated populations may experience drift or maladaptation despite available variation, whereas large, well-connected populations can maintain adaptive alleles and gene flow [135-138]. For example, forecasting predictions suggest that increasing connectivity or human-assisted gene flow among white-tailed jackrabbit populations may accelerate the evolutionary rescue of maladapted predominantly winter-white populations [107].

Finally, the resulting phenotype defines both the strength of selection and the likelihood of persistence. Species with discrete, binary morphs (e.g., white vs. brown) may face heightened extinction risk as snow duration declines, because mismatched individuals suffer greater predation (see Section "The cost of color mismatch"). In contrast, species expressing continuous winter color variation show greater adaptive capacity [107]. Intermediate phenotypes can act as a selective bridge between extremes, facilitating gradual frequency shifts and promoting evolutionary rescue under climate change [131]. However, empirical estimates of the fitness and frequency of these intermediates in natural populations remain scarce, underscoring the need for integrative field and genomic studies.

## Modeling Evolutionary Adaptation in SCC Systems

Forecasting the likelihood of evolutionary rescue in SCC species requires models that connect environmental change, genetic architecture, and adaptive responses through time. A previous large-scale effort by Mills, et al. [14] used ecological niche modeling (ENM) across eight mammal species to predict the current distribution of winter color morphs under changing snow conditions throughout species distribution ranges. Their results revealed clear geographic gradients from regions with winter-white individuals to regions with winter-brown individuals, including transition zones where both morphs coexist, suggesting that adaptation from standing variation could mitigate mismatch risk. Although ENMs have been instrumental in identifying climate-driven winter morph distribution patterns and areas with greater predicted adaptive shifts, they are largely correlative and do not incorporate genetic or adaptive processes, limiting their ability to predict true adaptive potential [139,140].

Other modeling approaches offer more mechanistic perspectives and are best applied in combination with each other. Genotype–environment (GE) association models can identify genomic regions associated with environmental gradients, pinpointing where selection may be acting even in the absence of fitness data [8,141]. Demographic and coalescent models reconstruct historical population dynamics and selective events, providing temporal context for contemporary adaptation [142,143]. Individual-based models (IBMs) simulate genotypes, selection, and ecological interactions across generations, allowing allele frequency trajectories to be estimated under varying scenarios of drift, migration, and selection [144,145].

Building on that, Ferreira, et al. [107] provided an integrative framework combining SCC polymorphism, ENMs, demographic models, and forward-in-time IBMs in SLiM [146] to predict evolutionary rescue in white-tailed jackrabbits. The ENM mapped spatial probabilities of winter color morphs for current and future climates, the latter informed by future climate forecasts. These projected mismatch scenarios informed forward-in-time simulations, which were parameterized with modelled demographic parameters and empirical-based genotypes and phenotypes. Results demonstrated that even low-frequency winter-brown alleles can drive rapid adaptation under declining snow cover, underscoring the key contribution of standing adaptive genetic variation for population persistence.

Future SCC modeling should extend this framework by incorporating spatial and temporal environmental heterogeneity and empirical species-specific estimates of camouflage mismatch fitness costs, while refining our understanding of genetic architecture, to produce more realistic predictions of adaptive limits and identify populations most at risk [9]. Historical records and Natural History Collections provide valuable temporal data for model calibration, revealing past shifts in allele and phenotype frequencies [147]. Moreover, SCC systems uniquely allow direct quantification of selection in the wild, as camouflage mismatch visibly affects predation and survival [57,70]. These empirical data provide rare opportunities to calibrate evolutionary models with real fitness information, helping define thresholds beyond which adaptation may fail to ensure population persistence. However, such data remain difficult to obtain, and emerging frameworks that integrate vital-rate estimates with genotype-environment (GE) models offer a promising way forward [2].

## Informed conservation actions

Genetic and evolutionary insights are important guides for conservation programs [2]. Although no program has yet implemented these approaches explicitly for SCC systems, this trait provides a clear path to do so. In SCC species, evolutionary rescue could occur when adaptive winter-brown variants increase rapidly enough to restore positive population growth in regions dominated by winter-white individuals under shorter snow seasons. This can be aided by genetic rescue through managed gene flow that introduces genetic diversity and, most importantly, adaptive alleles improving camouflage matching [14].

Classic genetic rescue examples illustrate the demographic benefits of increased heterozygosity: translocations revived prairie chickens after a severe bottleneck [148], and Texas pumas introduced into the isolated Florida panther population reduced inbreeding and temporarily lowered extinction risk [149,150]. Yet demographic recovery alone may not ensure long-term persistence unless the introduced variation also increases adaptive potential under contemporary selection [4,8]. This is the bridge to evolutionary rescue, where population recovery depends not just on neutral genetic diversity but on the spread of the adaptive variance that enhances fitness in changing environments [125].

Translating these principles to SCC systems requires a practical, testable roadmap for linking evolutionary potential to conservation action. First, dissect the genetic basis and evolutionary history of adaptive variants underlying SCC polymorphisms. Second, map the current and projected distributions of adaptive SCC variation relative to future climatic conditions [3,14,107]. Genetic markers linked to SCC variants can also serve as tools for genetic monitoring — for instance, through non-invasive approaches such as scat or eDNA sampling, supported by rapid assays or streamlined genomic pipelines — to track the frequency of adaptive alleles through time and space [151-153]. Such efforts can help validate model forecasts and identify populations lacking key adaptive variants. Third, prioritize conservation actions for populations that already harbor adaptive alleles [14,107]. Fourth, design adaptive connectivity strategies that maintain or restore gene flow along corridors predicted to favor winter-brown alleles, while assessing the risks of swamping or outbreeding depression [154]. In regions where key adaptive variants are absent, assisted gene flow or targeted reintroductions could be implemented to seed the standing variation needed for evolutionary rescue.

To implement this roadmap, developing standardized pipelines and practitioner-oriented tools will be essential, ranging from rapid DNA assays to decision-support frameworks that translate complex genomic and forecasting information into actionable management. These resources enable conservation actions that effectively maintain or restore adaptive potential in SCC populations facing accelerated snow loss, while also providing a transferable framework for other adaptive traits and climate-sensitive systems (Box 4).

### BOX 4. BEYOND SEASONAL CAMOUFLAGE: GENERAL APPLICABILITY OF THE LESSONS LEARNED

Seasonal color change (SCC) and winter color polymorphism provide a rare opportunity to directly observe and quantify climate-driven adaptation. However, while few species exhibit such visually trackable, discrete, and genetically well-characterized traits, the insights gained from SCC extend far beyond this specific system. Studying SCC helps uncover generalizable principles of phenotypic mismatch, evolutionary constraints, and the role of standing genetic variation in climate adaptation, all of which apply to species with less obvious adaptive traits.

SCC serves as a natural laboratory for testing evolutionary rescue, offering a measurable way to track how populations respond to rapid environmental change. It provides a framework for estimating fitness consequences of maladaptation, identifying evolutionary tipping points, and integrating genomic and ecological data into predictive models. These insights are broadly relevant to conservation, as most species will face environmental mismatches due to changing climates [155] but lack the clear visual markers that make SCC species so tractable.

Furthermore, SCC research integrates key methodologies – including genomic analyses, predictive modeling, and real-time monitoring – that can be adapted to study other seasonal traits, such as hibernation, reproduction, and migration timing. Since the first genetic study of SCC in 2002 [156], major advances in genomics and landscape ecology have refined the ability to link genotype, phenotype, and fitness outcomes, demonstrating how genetic variation can facilitate or constrain adaptive responses.

More broadly, the lessons learned from SCC-based conservation efforts can be expanded to other species, informing actions to mitigate climate-driven biodiversity loss by enhancing adaptive management, targeted genetic monitoring, and conservation prioritization.

## Concluding remarks & future perspectives

The SCC system is a powerful model for studying climate-driven adaptation, offering a unique opportunity to integrate evolutionary biology with conservation practice in a rapidly changing world (Box 4). While genomic advances have significantly expanded our understanding of SCC polymorphism, realizing their full conservation potential requires addressing key gaps in data and application. Moving forward, several challenges must be tackled to maximize the impact of evolutionary research on conservation action:

1. Closing Taxonomic and Knowledge Gaps: Despite growing genomic datasets, significant taxonomic gaps remain (Table 1), with some SCC species still lacking high-resolution genetic data and genetic studies. At the same time, for species where data exist, deeper investigation is needed to understand key aspects of their evolutionary history, adaptive potential, and conservation status. Expanding both taxonomic breadth and species-specific insights will strengthen predictions and refine conservation priorities.
2. Bridging Fitness Data Gaps: A major challenge in predicting evolutionary rescue is the lack of direct fitness data. While studies like that of Mills, et al. [14] have identified global hotspots for evolutionary rescue, and Zimova, et al. [70] have quantified the cost of mismatch, empirical data on survival, reproduction, and selection pressures remain limited. Longitudinal studies integrating genomic, ecological, and demographic data will be essential for improving predictions of adaptive potential.
3. Improving Forecasting Models: Current ecological niche models provide valuable predictions but often fail to incorporate adaptive potential and genetic constraints on evolution. Future research should refine genotype-phenotype-fitness informed forecasting models, improving accuracy for predicting species' resilience or vulnerability under climate change.
4. Developing Proactive Conservation Strategies: Conservation efforts must prioritize populations with high adaptive potential to enhance long-term resilience. Adaptive management approaches, informed by genomic and ecological insights, are critical for mitigating climate-driven biodiversity loss. Strengthening collaboration between evolutionary biologists, conservation practitioners, and policymakers is fundamental to ensure that research translates into actionable conservation strategies.

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## Author contributions

J.M.F., J.M.G. and L.S.M conceived the project; M.M.A., J.M.F., J.M.G., and C.K.S.U. conceptualized the manuscript; M.M.A., C.K.S.U., M.S.F., and I.M. conducted the literature review and data curation; J.M.F., J.M.G., and J.P. supervised the work; M.M.A. led writing, with section-specific contributions from M.M.A., I.M., C.K.S.U., M.S.F., J.P., and P.C.A, and review of J.M.F., J.M.G. and L.S.M.; All authors revised and edited the final version of the manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

The online version contains supplementary material detailing Table 1 for each SCC species.

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