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Molecular mechanisms of adaptive evolution in wild animals and plants

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Wild animals and plants have developed a variety of adaptive traits driven by adaptive evolution, an important strategy for species survival and persistence. Uncovering the molecular mechanisms of adaptive evolution is the key to understanding species diversification, phenotypic convergence, and inter-species interaction. As the genome sequences of more and more non-model organisms are becoming available, the focus of studies on molecular mechanisms of adaptive evolution has shifted from the candidate gene method to genetic mapping based on genome-wide scanning. In this study, we reviewed the latest research advances in wild animals and plants, focusing on adaptive traits, convergent evolution, and coevolution. Firstly, we focused on the adaptive evolution of morphological, behavioral, and physiological traits. Secondly, we reviewed the phenotypic convergences of life history traits and responding to environmental pressures, and the underlying molecular convergence mechanisms. Thirdly, we summarized the advances of coevolution, including the four main types: mutualism, parasitism, predation and competition. Overall, these latest advances greatly increase our understanding of the underlying molecular mechanisms for diverse adaptive traits and species interaction, demonstrating that the development of evolutionary biology has been greatly accelerated by multi-omics technologies. Finally, we highlighted the emerging trends and future prospects around the above three aspects of adaptive evolution.

adaptive evolution, adaptive trait, coevolution, comparative genomics, convergent evolution, genetic convergence, molecular mechanism, mutualism, parasitism, phenotype convergence

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Introduction

Adaptive evolution is one of the important strategies of species survival and persistence and is the main subject of evolutionary biology. Uncovering the molecular mechanisms of adaptive evolution can help understand the formation of adaptive traits and the intrinsic relationships of species diversification, phenotypic convergence, and inter-species interaction, thus, providing valuable insights into the formation and persistence of biodiversity. For a long time, due to a lack of reference genomes for non-model organisms, adaptive evolution studies were mainly limited to model organisms or non-model organisms but used the candidate gene methods. With the development of next-generation sequencing technologies, more and more genomes have been sequenced for non-model organisms. The arrival of the genomics era has made it easier to uncover the molecular mechanisms of adaptive evolution at the genomic level for non-model organisms and to explore the underlying genetic basis of many interesting adaptive traits without pre-existing knowledge of related candidate genes.

In this review, we present the recent advances in the molecular mechanisms of adaptive evolution in wild animals and plants, focusing on three aspects of trait evolution, namely adaptation, convergent evolution, and coevolution, and discuss development trends and potential research hotspots. First, we focus on the adaptive evolution of important traits such as morphological, behavioral, and physiological traits in different taxonomic groups of wild animals and plants. Second, we discuss advances in convergent evolution in response to extreme environments, echolocation convergence, and dietary convergence in wild animals and highlight advances in the understanding of convergent evolution in response to abiotic and biotic stresses in wild plants. Third, we summarize the recent research advances in the four types of coevolution in wild animals and plants: mutualism, parasitism, predation, and competition. Last, we highlight some methodological advances and future prospects in the above three aspects of adaptive evolution.

Adaptive mechanisms of functional traits in wild animals and plants

During the long history of evolution, organisms on the earth have developed various phenotypic traits to cope with the changing climatic and geographic conditions in order to survive and thrive. As a result, species from all kingdoms of life have prospered and together form the current diverse biosphere. They each obtained common or unique functional traits to facilitate their occupation of ecological niches, which is regarded as adaptation. Although most adaptive phenotypic traits have been described since Darwin's work, the exploration of the underlying molecular mechanisms began not long ago and accelerated in the past two decades due to the explosion of genomic data. Here we summarize the recent advances in adaptive evolution and its molecular basis, primarily focusing on wild animals and plants.

Crosstalk between phenotypic traits and terrestrial animal adaptation

The earth has rich geographical environments and provides complex and diverse habitats for terrestrial animals. To fit in the varying habitats, animals have developed various strategies to interact with the different environmental conditions they encounter. This can happen at different levels and is most obviously reflected by a series of phenotypic changes such as morphological, physiological and behavioral changes. These phenotypic changes help animals occupy unique ecological niches, facilitating their propagation. In the past few decades, rapid progress in omics technologies and the development of analytical tools greatly improved our knowledge about the underlying molecular mechanisms of those phenotypic changes, promoting our understanding of animal adaptation.

Molecular mechanisms underlying morphological adaptation

Morphological changes are the most evident observations in species living in a specific ecosystem. For example, the giant and red pandas have evolved pseudo-thumbs to help grasp bamboo for feeding; bats have developed patagium, which enables their powerful flight. A classic example of morphological adaptation is Darwin's finches, well-known for their diverse shapes and sizes of beaks, which are believed to facilitate the exploitation of particular types of food, including fruits, seeds, insects, nectar, and pollen (Abzhanov et al., 2004). These morphological adaptations enable the finches to fill a variety of ecological niches with different food sources. Although morphological studies on Darwin's finches have been conducted extensively for centuries (see Abzhanov, 2010), the molecular components controlling beak shapes remained elusive until a key gene was identified in 2004. Differential expression of bone morphogenetic protein 4 (*Bmp4*) during embryo development is highly correlated to beak morphology, i.e., species with blunt beaks exhibited higher Bmp4 levels at earlier stages than those species with pointed beaks (Abzhanov et al., 2004). Artificial modulation of Bmp4 level in chicken embryos confirmed its role in deep and broad beak shape formation (Abzhanov et al., 2004; Wu et al., 2004). Subsequently, more molecular elements influencing beak morphology have been gradually identified, including calmodulin (CaM), a Ca^{2+} signaling component (Abzhanov et al., 2006), *ALX1* locus encoding a transcription factor (Lamichhaney et al., 2015), and 11 SNPs linking with beak size (Chaves et al., 2016). Recently, a large-scale comparative genomics study revealed that 1,434 protein-coding genes and 39,806 noncoding elements may be involved in craniofacial development (Yusuf et al., 2020), pushing the exploration of Darwin's finches into the genomics era. Altogether, current data suggest that besides key protein-coding genes, regulatory elements also played important roles in morphological adaptation.

Coat pigmentation is another characteristic that has fascinated scientists for hundreds of years (Hoekstra, 2006). Coloration is usually considered a strategy for camouflage for animals to conceal themselves, either to hunt or to avoid being preyed on (Protas and Patel, 2008). Animals, therefore, developed corresponding coat colors to blend in with the surroundings of their natural habitat. Rock pocket mice from the southwestern United States and northern Mexico provide a typical example. This species, with a sandy dorsal pelage, predominantly inhabits light-colored rocks. However, some populations with dark-colored dorsal furs are found on lava flows (Nachman et al., 2003), indicating an adaptation to their living environments. In addition, coloration could be an effective tool for warning/startling predators, conspecific communications, and even regulation of physiological processes (Protas and Patel, 2008). It is common for insects to use colors and patterns to keep predators away, e.g., the bright yellow, orange, red, and black colorations in some bees and ants and the brightly colored area on the hindwings of some moths are their warning signals to potential predators (Protas and Patel, 2008). Colorful plumages in male birds (Siefferman and Hill, 2003), and colored skin patches in some primate females (Domb and Pagel, 2001), reflect the status of an individual for mating choices and play a role in information exchange. Coat color may also contribute to body temperature regulation, as demonstrated by three different color morphs of springbok (Hetem et al., 2009); dark skin color can prevent UV radiation from causing oxidative DNA damage (Li et al., 2013).

Although there is a great diversity of coloration phenotypes among animals, it is surprising to see that many of them can be characterized by the molecular variants of the Melanocortin-1 receptor (*MC1R*) gene (Eizirik et al., 2003; Sturm et al., 2003), despite the fact that more than 150 genes influencing pigmentation have been identified (Hofreiter and Schöneberg, 2010). The ratio of eumelanin and pheomelanin, which determines the dark or light color, primarily depends on the binding of MC1R and its two ligands: α-MSH binding activates MC1R and leads to eumelanin production, while Agouti signaling protein binding inhibits MC1R, resulting in pheomelanin production (Caro and Mallarino, 2020). Mutations in *MC1R* or *Agouti* coding sequences are responsible for variation in coloration (Barrett et al., 2019; Eizirik et al., 2003; Hoekstra et al., 2006; Sturm et al., 2003). However, in the rock pocket mice, *MC1R* mutations could explain the dark-colored fur in one lava flow-dwelling population but not in another (Nachman et al., 2003), suggesting independent evolution of coat color in this species and highlighting the contribution of other genetic factors. With the rapid progress in DNA sequencing technologies and computational theories and practices, the veil of the genomic basis of coat pigmentation has been uncovered gradually in recent decades. Genome-wide scans have identified a group of positively selected genes associated with unique color patterns in certain species (Figueiró et al., 2017; Gao et al., 2018). Additionally, regulatory alterations and introgressions are important factors affecting animal coloration (see reviews in Eizirik and Trindade, 2021; Orteu and Jiggins, 2020), suggesting that coloration is a complex trait involving many molecular factors. As technology advances, we expect to unveil a finer-resolution molecular basis underlying the dramatic morphological variations in the future.

Molecular mechanisms underlying physiological adaptation

Physiological alteration is another strategy that animals adopt to cope with environmental stressors. For example, the giant panda exhibits an exceptionally low daily energy expenditure, possibly controlled by a unique mutation in the *DUOX2* gene that reduces thyroid hormone levels (Nie et al., 2015). This physiological change was confirmed through a mutated mouse model (Rudolf et al., 2022). This might be one of the reasons why the giant panda can survive on a specialized bamboo diet. Physiological adaptation is particularly important to species experiencing fluctuations in environmental conditions, such as migratory birds and hibernating animals. Migratory birds can reduce metabolic rate during long-distance flight while generating thrust by the locomotory muscles with unusually high efficiency. They can also minimize body mass through digestive organs atrophy and increasing lipid storage before their migration (Weber, 2009). Similarly, hibernators can greatly reduce their metabolic rate and body temperature to survive environmental stressors such as climatic extremes and lack of food and water. During the past two decades, the thirteen-lined ground squirrels were extensively studied as model animals to dissect the molecular and genetic basis of hibernation. Metabolomic profiling revealed seasonal changes of small molecules circulating in their blood (D'Alessandro et al., 2017), suggesting the cleaning of toxic metabolic wastes and replenishing of necessary metabolic substrates in the torpor-arousal cycles (Andrews, 2019). The phenotypic fluctuation between the long bouts of hypothermic torpor and the brief normothermic interbout arousals are a result of gene expression regulation. Eight genes are down-regulated, and two genes are up-regulated during the torpor period, which may contribute to the lowered physiology level. For example, *HIST1H1C*, encoding an H1 histone that often inactivates proximal genes by increasing chromatin compaction, shows significant global upregulation during the torpor (Andrews, 2019). The ground squirrel transcriptome browser includes mRNA expression information for 14,261 genes (https://www.d.umn.edu/~mhampton/GB18.html), and more candidates involved in hibernation regulation are expected to be identified in the future. In addition to regulation at the gene expression level, post-translational protein modifications may play a role in protein activity alteration, as proteomics has revealed the stability of the proteome, even across the physiological shifts of torpor-arousal cycles (Grabek et al., 2015). Also, a recent report emphasized the role of genetic variation in the seasonal onset of hibernation by genome-wide association scan (GWAS) and expression quantitative trait loci (eQTL) analyses in 153 ground squirrel individuals (Grabek et al., 2019). As a trait related to temperature, hibernating animals are known for their cold tolerance during hibernation. Functional assays demonstrated that the cold sensitivity of the ground squirrel TRPM8 can be reduced to a temperature range below 10°C, whereas TRPM8 in rats is activated at temperatures below 26°C (Matos-Cruz et al., 2017). Six amino acid substitutions in the transmembrane core of ground squirrel TRPM8 are responsible for the sensitivity alteration (Matos-Cruz et al., 2017), highlighting the importance of genetic composition for the physiological adaptation in hibernation again.

In recent decades, plateau adaptation emerged as another topic attracting much attention. Due to the extreme ambient temperatures, hypoxia and UV radiation on the plateau, indigenous animals evolved extraordinary features to overcome the harsh conditions, mainly through physiological responses. For example, to cope with hypoxia, highland natives, including humans and other mammals, generally exhibit increased hemoglobin content and strengthened heart function to increase capacity for oxygen transportation (Beall, 2014; Storz and Cheviron, 2021). The hypoxia-inducible factor (HIF) signaling pathway is a target for selection in various native highland human populations and other indigenous mammals and birds (Beall et al., 2010; Schweizer et al., 2019). HIF genes like *EPAS1* (encoding HIF2α) and *EGLN1* (encoding PHD2) possibly regulate the expression of other genes in an O_2-dependent manner and thus mediate the plastic responses to hypoxia (Storz and Scott, 2021). A recent study also suggested that the *Retsat* gene might be an important candidate gene underlying convergent adaptation to hypoxia among Qinghai-Tibet Plateau indigenous mammals (Xu et al., 2021a). Despite these features in common, plateau natives also demonstrate distinctive characteristics. For example, Tibetans prefer glucose as their metabolic fuel, as their *PPARα* variants are associated with a reduced capacity for fatty acid oxidation (Horscroft et al., 2017). Meanwhile, small highland animals like deer mice tend to utilize lipids as their primary metabolic fuel source (Cheviron et al., 2012), probably to enhance their thermogenic capacity for body temperature maintaining under the extreme coldness on the plateau. Even within the same species, heterogeneity exists among populations, as exemplified by plateau zokors, in which extremely high-altitude populations (>3,700 m) maintain elevated heart mass to body mass ratio or altered erythrocytes (2,700–3,700 m) (Zhang et al., 2021), likely associated with a group of corresponding positively selected genes in these populations. Overall, the physiological adaptation to plateau appears to be a complex process involving not only constitutive genetic evolvement but also facultative regulation, seemingly impacted by heterogeneous stressors. There is a need for comprehensive studies on both wild species and model animals to gain insights into mechanisms of plateau adaptation.

Molecular mechanisms underlying behavioral adaptation

Animals behave differently because they live in diverse habitats requiring different behavioral adaptations. Several previous studies have reported amazing behaviors in the animal kingdom, drawing admiration for the marvelous work of nature and raising curiosity about its underpinning mechanisms. Driven by a combination of progress in multidisciplinary studies and methodological advances, our knowledge of animal behavioral adaptation has expanded in recent years. For example, a New World monkey, the white-faced saki, primarily feeds on unripe fruit and its seeds, a specialized behavior enabling them to occupy a unique ecological niche that prevents competition from sympatric frugivores (Kinzey, 1992). However, this behavioral adaptation exposes them to a higher risk of encountering greater amounts of toxins because newly formed plant tissues generally contain the highest level of cyanogenic glycosides in such toxin-containing plants (Gleadow and Møller, 2014). A recent integrated study revealed that saki monkeys have developed an extremely high sensitivity to toxic β-glucopyranosides via a single amino acid substitution in their bitter taste receptor Tas2R16, conferring them the ability to avoid such toxin-containing plant species when foraging (Yang et al., 2021). Another intriguing case is the extraordinary obsession of the giant pandas with fresh horse manure; they roll in such dunghills and rub feces all over their bodies (Zhou et al., 2020). This unusual behavior was ascribed to the chemical BCP/BCPO (beta-caryophyllene/caryophyllene oxide) found in fresh horse manure and can inhibit the cold-activated ion channel TRPM8. Thus, giant pandas might temporarily tolerate low temperatures via inhibition of the cold-sensitive channel (Zhou et al., 2020). Unlike these cases directly linked to genetics, behavioral adaptation is a complex trait involving multiple systems of the body, making the exploration of its genetic basis practically difficult. So far, efforts to elucidate the molecular mechanisms of behavioral adaptation have been limited to relatively few species (Bubac et al., 2020). Progress in understanding echolocation in mammals has been made in the last few decades. To echolocate, the echolocating species must have at least three abilities: to make and direct the high-frequency calls, to hear the returning echoes, and to process the information (Teeling, 2009). This process involves vocalization, hearing, and neural processing systems. In bats, a model echolocating species, the first "vocalization" gene *FOXP2* (Li et al., 2007) and the first "hearing" gene *Prestin* (Li et al., 2008) were identified, and subsequent studies ascertained the critical functional sites and elucidated their evolutionary trajectories (e.g., Li et al., 2017; Liu et al., 2012; Liu et al., 2014). Examination of the neurobiology of echolocating bats further revealed neural processing in response to the echo feedback and their interactive dynamics (Luo and Moss, 2017; Moss and Sinha, 2003), complementing our knowledge of bat echolocation. A recent study integrated behavioral tests, anatomy evidence, evolutionary molecular analyses, and functional assay verification to discover a new echolocating mammal, the soft-furred tree mice (He et al., 2021), providing a research paradigm including molecular techniques to underpin complex behaviors.

Adaptive mechanisms of aquatic animals

Water bodies cover approximately 70% of the surface of the earth, providing the habitat for numerous aquatic animals, including invertebrates (e.g., mollusks and crustaceans) and vertebrates (e.g., fish and cetaceans). These species with different phylogenetic backgrounds must conquer ecophysiological difficulties and adapt to the aquatic environment. Thus, adaptations of animals to the aquatic habitat are one of the fascinating aspects of nature. Adaptations to distinct challenges, including reduced brightness, changes in the olfactory system, distinct pathogens, temperature changes, osmotic pressure regulation, and hydrostatic pressures, are of great interest (Figure 1).

Sensory adaptation

Sensory systems evolve and enable aquatic animals to perceive the unique set of cues relevant to their survival (Oteiza and Baldwin, 2021). A number of comparative studies have uncovered the molecular basis of receptor properties and identified sensory strategies in aquatic animals. For example, the deletion of the gene *Mpv17* and the specific amino acid substitutions of *Ush2a* in *Sinocyclocheilus* cavefishes indicated that their weak hearing evolved in caves (Yang et al., 2016). Conversely, the expanded genes in Shaw's sea snake (*Hydrophis curtus*) were enriched in functions associated with hearing, indicating the enhancement of their low-frequency auditory sensitivity in the open ocean (Peng et al., 2020).

On the other hand, general degradation of olfaction has occurred in aquatic animals. The snailfish from the Yap Trench has a contracted olfactory receptor gene family and less functional olfactory receptor genes (Mu et al., 2021). Similarly, less functional olfactory receptor genes are also found in penguins (Lu et al., 2016), suggesting a degraded sense of smell. To adapt to various photic environments in the water, such as dark bathypelagic zones and bright shallow open waters, aquatic animals use different molecular mechanisms. In snailfishes and cavefishes living in the dark, the number of lens-related genes decreases, the number of pseudogenes associated with melanogenesis increases, or the expression of eye development-related genes and transcription factors decreases (Mu et al., 2021; Wang et al., 2019; Yang et al., 2016). On the contrary, in Neotropical cichlid fishes living in a much brighter water environment, the unique opsin expression pattern provides molecular insights into their specific vision adaptation (Torres-Dowdall et al., 2021).

Immune adaptation

Aquatic animals are exposed to more different pathogenic microorganisms than their terrestrial relatives. The evolution of the immune system, composed of innate and adaptive immunity, has become an important adaptation for aquatic animals (Storey and Jordan, 2008). For example, comparative genomic analyses of Shaw's sea snake showed that the expanded gene family is mainly enriched in the Nod-like receptor signaling pathway, and 31 significantly expanded genes and five positively selected genes are found in the proteasome pathway (Peng et al., 2020). Both of these pathways play a crucial role in the immune and inflammatory responses, suggesting that Shaw's sea snake evolved a strong immune system to deal with pathogens from the ocean environment. A recent study found that the tumor necrosis factors, the gamma-interferon-inducible lysosomal thiol reductase, and the major histocompatibility complex class II transactivator families, which are involved in the immune response, expanded in the large yellow croaker (*Larimichthys crocea*), indicating the evolutionary trend of innate and adaptive immunity (Wu et al., 2014). Additionally, the pathogen binding domains of serum *tf* (transferrin), a key gene in the innate immune system, was positively selected in freshwater turtles (Liu et al., 2018). These lines of evidence imply that different animal taxa have evolved enhanced immune mechanisms to cope with hazards in the aquatic environment.

Temperature sensitivity

Changes in environmental factors resulting from the transition of niches in the process of speciation and global warming have prompted organisms to adapt to the temperature in their own habitat (Dhaka et al., 2006). The diversity of habitat temperatures is one of the driving forces for aquatic animals to evolve different temperature sensitivities.

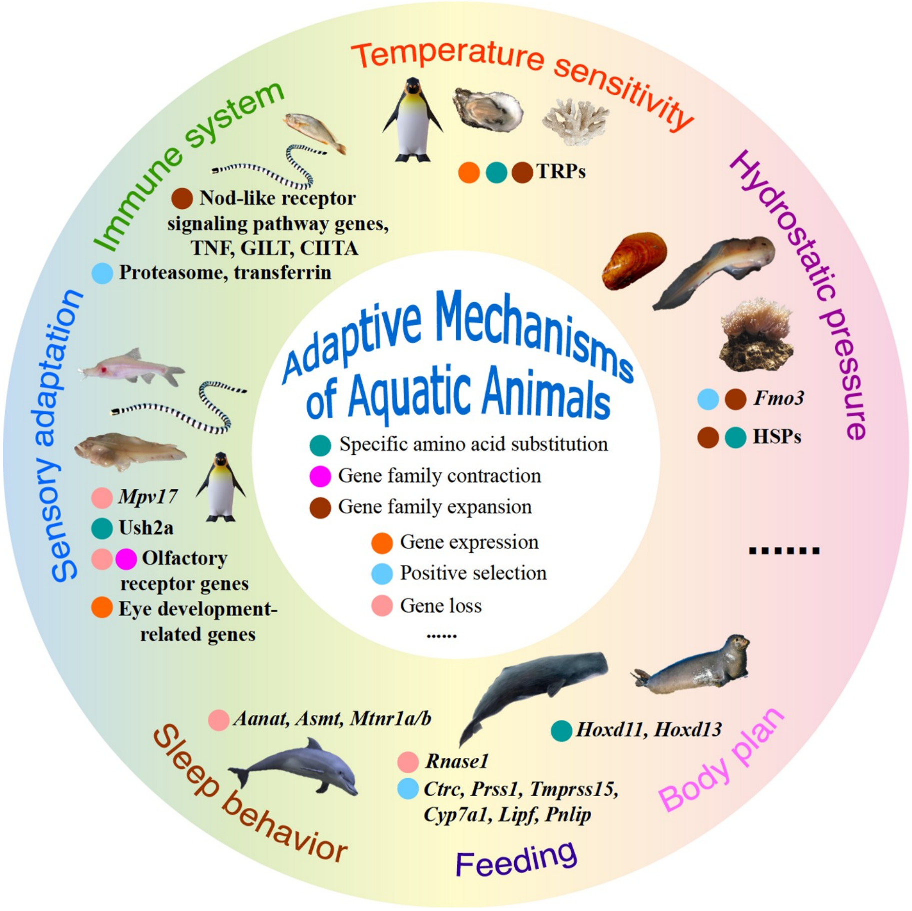

Figure 1 Summary of molecular adaptive mechanisms of aquatic animals. Circles with respective colors show different types of molecular change in genes or proteins identified in certain aquatic animals, following the adaptation categories of hydrostatic pressure, temperature sensitivity, immune system, sense, sleep, feeding and body plan, respectively.

In order to survive, thermal adaptation is one of the critical ecological pressures that organisms must face. Some members of the TRP (Transient Receptor Potential) superfamily use peripheral thermosensation as the main mechanism of thermal adaptation (Vriens et al., 2014). Single amino acid mutations are one of the molecular mechanisms for different thermal adaptations between species. For example, the emperor penguin (*Aptenodytes forsteri*) living in the Antarctic has much lower cold sensitivity compared with the African elephant (*Loxodonta africana*) because the *TRPM8* of the penguin exhibits remarkable tolerance to low temperatures caused by amino acid mutations with distinct side-chain hydrophobicity in the pore domain (Yang et al., 2020). A total of 66 members of the TRP superfamily were identified in the Pacific oyster (*Crassostrea gigas*) genome (Fu et al., 2021), implying that TRP gene expansion is one of their mechanisms to adapt to the high-temperature environment. Additionally, the adaptation of gene expression to the thermal environment is also an evolutionary path. Different coral holobionts under heat stress display specific expression levels of photosynthesis-related genes and exhibit different thermal sensitivities when exposed to the same thermal conditions (Avila-Magaña et al., 2021).

Adaptation to hydrostatic pressures

Aquatic environments provide a wide range of hydrostatic pressures (HP), increasing by 1 atm per 10 m of depth in the ocean, which perturbs many cellular processes, for example, by rigidifying membranes and disturbing protein folding and ligand binding (Macdonald, 2021). Therefore, it is puzzling how aquatic animals can withstand when they are exposed to a high HP environment. Trimethylamine N-oxide (TMAO), which increases with depth in marine fishes and crustaceans (Yancey, 2020), has a protein-stabilizing ability by restoring denatured proteins to their native structure (Ma et al., 2014). Gene duplication of the gene flavin monooxygenase 3 (*fmo3*), which codes for the enzyme TMAO, has been observed in most teleost genomes (Wang et al., 2019). Moreover, the positively selected *fmo3a* gene is strongly expressed in the liver of the deep-sea snailfish (*Pseudoliparis swirei*) (Wang et al., 2019). These changes may help the deep-sea snailfish increase intracellular TMAO levels under high HP to enhance protein stability. Stress proteins such as heat shock proteins (HSPs, hsp70, hsp90) play an important role in protein homeostasis by stabilizing cellular functions (or facilitating damaged protein degradation) under pressure (Tkáčová and Angelovičová, 2012). The deep-sea snailfish has five copies of the gene *hsp90*, and its specific amino acid substitution (alanine-to-serine) lies in close proximity to the ATP-binding pocket, which may contribute significantly to a local structural interaction affecting hsp90 activity (Wang et al., 2019). Similarly, expansion of the *hsp70* gene family observed in the deep-sea mussel (*Bathymodiolus platifrons*) may be a genetic resource allowing them to cope with HP (Sun et al., 2017). Cholesterol is a key constituent of cell membranes, and increasing its content helps maintain the fluidity of membranes under high HP (Bernsdorff et al., 1997). Interestingly, the parallel evolving genes (e.g., *HDLBP*) detected in the deep-sea anemone (*Paraphelliactis xishaensis* sp. nov.) and mussel are involved in cellular cholesterol transport and metabolism, implying that these deep-sea animals have convergent adaptations in membrane lipids and cholesterol under stress conditions (Feng et al., 2021).

Secondary aquatic adaptations in marine mammals

Marine mammals, including cetaceans, pinnipeds, and manatees, are a highly specialized group of mammals that returned from the land to the ocean and ultimately became a successful and highly diverse group of aquatic mammals (Berta et al., 2005). Living in water poses new challenges, such as changes in locomotion, body plan, vision, olfactory and auditory sensation, feeding, environmental osmotic pressure, sleep behavior, combating new pathogens, and hypoxia. The molecular bases of these radical phenotypic transitions have been widely explored thanks to the advances in genomic technologies and evolutionary genetics (Foote et al., 2015; McGowen et al., 2014; Yuan et al., 2021). For example, the body plan of marine mammals has been streamlined for ease of swimming. In cetaceans, the forelimbs develop into short flippers, phalanges develop with a great difference in number, and hindlimbs degenerate (Cooper et al., 2007). The *Hox* (Homebox) gene family is responsible for mammalian limb development, and mutations in the gene *Hoxd11* cause defects in specific bones of the limbs, including the carpal and tarsus (Davis and Capecchi, 1994; Favier et al., 1995). Distinctive amino acid substitutions (G110S and D223N) have been recorded in cetacean Hoxd11, consistent with the loss of hindlimbs in the common ancestor of cetaceans and providing molecular evidence for the adaptive evolution of *Hoxd11* in cetacean limb morphology (Li et al., 2020b). Another study found that cetacean Hoxd13 has two or three more repeats of alanine residues (Wang et al., 2009). Moreover, recent functional tests revealed overexpression of the cetacean Hoxd13 in zebrafish and significant changes in gene expression in Wingless/Integrated (Wnt) and Hedgehog signaling pathways, further emphasizing the important role of Hoxd13 in cetacean flipper formation (Sun et al., 2021).

Perfect osmoregulation ability is the basis for marine mammals to resist osmotic stress. After entering the ocean, marine mammals faced selective pressures for continued efficient and powerful kidney function, and the entire salt load and water loss they experienced could be offset by the production of concentrated urine (Bradley, 2009). The study of osmoregulation-related genes in cetaceans showed that *SLC14A2* (Urea transporter A), *AQP2* (Aquaporin 2), *ACE* (Angiotensin I converting enzyme), and *AGT* (Angiotensinogen) have significant positively selected signals exclusive to cetaceans, suggesting that cetaceans may maintain water balance by enhancing the transport of water and urea to concentrate urine (Xu et al., 2013). The RAAS (Renin-angiotensin-aldosterone) system that plays a key role in the balance of electrolytes, especially the reabsorption of sodium ions, has undergone adaptive evolutionary changes in a hypertonic environment (Ortiz and Worthy, 2000; Xu et al., 2013). Detection of positive selection in the gene encoding the urea transporter protein SLC14A2 (known as *UT-A2*) in the Yangtze finless porpoise (*Neophocaena asiaeorientalis*), identification of a new copy of *AQP2* in Delphinoidea, and overexpression of AQP2 in the kidney of finless porpoise living in the ocean provide novel insights into the adaptation of osmoregulation in cetaceans (Kishida et al., 2018; Ruan et al., 2015; Wang et al., 2015). Additionally, three key genes (*ADCY1*, *DYNC2H1*, and *UTA2*) detected by genome-wide population analysis in marine finless porpoises are associated with renal water homeostasis, vasopressin-regulated water reabsorption and urea transport. The positive selection of *UTA2* and *ACE2* in the marine and Yangtze finless porpoises, respectively, might explain their adaptations to different brackish and freshwater environments and support the independent species status of the Yangtze finless porpoise (Zhou et al., 2018). In pinnipeds, reabsorption of water and electrolytes appears to be mediated by AVP (aldosterone and vasopressin) and RAAS, respectively, and may also require regulation of the pituitary-adrenal axis to replenish salt concentrations in the hyponatremic state (Ortiz, 2001).

The olfactory system of marine mammals has been greatly reduced. For instance, the pseudogenization of olfactory receptor genes has been reported in the genomes of minke whales and sperm whales (Kishida et al., 2007) and other cetaceans (McGowen et al., 2008). Moreover, with the transition from land to sea, marine mammals had to change their diet and feeding behavior. For instance, modern cetaceans have dramatically changed from herbivory to carnivory, accompanied by swallowing food without chewing for toothed whales and filtering for baleen whales. Pseudogenization of sweet, umami, and bitter taste receptor genes reported in cetaceans (Zhu et al., 2014) and loss or major reduction of umami taste sensation reported in pinnipeds (Sato and Wolsan, 2012) might be explained by the effects of dietary changes and feeding behavior of swallowing food whole without mastication. The dietary transformation of marine mammals also involves the adaptation of enzymes related to food digestion (Li et al., 2020a). Wang et al. (2016) found that protease (*CTRC*, *PRSS1*, and *TMPRSS15*) and lipase (*CYP7A1*, *LIPF*, and *PNLIP*) coding genes are positively selected, suggesting that cetaceans have evolved an enhanced digestion capacity for proteins and lipids, the major nutritional components of their prey (fishes and invertebrates). In addition, modern cetaceans have also lost the pancreatic *RNASE1* copy with digestive function, which conforms to the dietary change to carnivory (Wang et al., 2016).

Marine mammals evolved unihemispheric slow wave sleep (USWS), a different sleep behavior from that of terrestrial mammals, in which one cerebral hemisphere sleeps while the other stays awake. USWS allows marine mammals to have the benefits of sleep, breathing, thermoregulation, and vigilance. Loss of melatonin synthesis and receptor genes (i.e., *AANAT*, *ASMT*, and *MTNR1A/B*) may have been a precondition for adopting unihemispheric sleep (Huelsmann et al., 2019; Lopes-Marques et al., 2019; Yin et al., 2021). Melatonin, an endogenous hormone produced by the pineal gland, synchronizes circadian rhythms and improves the duration and quality of sleep (Zhdanova et al., 1997). Yin et al. (2021) identified independent inactivating mutations of *AANAT* in cetaceans and manatees and found that cetacean *AANAT* exhibited undetectable enzyme activity, which is favorable for disrupting the production of melatonin, thus contributing to increased wakefulness to adapt to completely aquatic environments. Furthermore, cetaceans have accumulated deleterious mutations in cortistatin (*CORT*), a neuropeptide involved in regulating mammalian biorhythm and slow wave sleep (Valente et al., 2020). The combined loss of melatonin and *CORT* signaling may have strongly contributed to the irregular circadian activity and sleep observed in cetaceans characterized by constant activity and alertness during USWS.

Adaptive evolution in plants

Genetic variation within species provides the evolutionary potential for the adaptation of plants to the changing environment. The development of sequencing technology has enabled the production of lots of high-quality sequences of plant genomes, providing a great opportunity to study adaptive evolution. In plants, four common methods used to study the mechanisms of adaptive evolution include comparative genomics, population genomics, association analysis between sequence variation and climate parameters, and studies of functional traits crucial for plant adaptation.

Adaptive evolution based on comparative genomics

Interspecific comparison of genomic sequences is a generally used method to study adaptive evolution in plants. There is a diversity of genomic variations across species, such as large structural variations (SVs), the insertion or deletion of sequences (indels) or transposable elements (TEs), short tandem repeats (STRs), copy number variations (CNVs), and single nucleotide polymorphisms (SNPs), which could affect genome size variation, gene expression, phenotype variation, and adaptation.

Whole-genome duplication (WGD) events frequently occur in the history of green plants and affect genome evolution and adaptation, and most green plants have experienced WGD events (Van de Peer et al., 2017). Owing to WGD, genomes suffered rapid genomic reorganization leading to "genome shock." For example, various numbers of chromosomes were observed in *Brassica napus* (Xiong et al., 2011). However, it has been shown that genomes of some polyploid species, such as cotton (*Gossypium*) and *Arabidopsis suecica*, are stable (Burns et al., 2021; Chen et al., 2020). The intrinsic karyotype stability plays an important role in the evolution of flowering plants, especially for polyploidy formation (Zhang et al., 2013). Furthermore, in allopolyploids, recombination between homoeologous chromosomes can affect epigenetic and gene expression variation and generates novel transcripts and proteins, which may contribute to genome evolution and adaptation (Li et al., 2019; Zhang et al., 2020b).

Genome size variation could be correlated with adaptation, and the organisms with bigger genome sizes might pay a higher cost to survive (Knight et al., 2005). There are huge genome size variations in plants, ranging from 12 Mb to 148.8 Gb (Greilhuber, 2005; Hidalgo et al., 2017), and genome size changes within a single genus or even species (Johnston et al., 2005). In the rice relative, *Oryza brachyantha*, the compact genome resulted from the low activity of long-terminal repeat retrotransposons and massive internal deletions of ancient long-terminal repeat elements (Chen et al., 2013). Similarly, the mangrove genomes revealed that the convergent TE load reduction contributed to smaller genome sizes (Lyu et al., 2018). Genome size variations are even observed within species; for example, the assemblies of seven *Arabidopsis* accessions revealed that there are 5 to 6 Mb non-reference sequences in each genome (Jiao and Schneeberger, 2020). A well-known hypothesis is that genome sizes expanded largely by the transposition of TEs or polyploidization. However, it is not clear which kinds of genetic elements and evolutionary mechanisms could account for the genome size variation between closely related species (Ai et al., 2012). The comparison between genomes of *A. thaliana* (~130 Mb) and its close relative *A. lyrata* (~200 Mb) indicates that a large number of deletions from intergenic regions contribute to the smaller genome of *A.*

thaliana, which are under natural selection (Hu et al., 2011).

Gene number variation is balanced by gene gain and loss, and "dosage balance" and "less is more" hypotheses are proposed to contribute to natural variations and adaptation (Birchler and Veitia, 2007; Edger and Pires, 2009; Olson, 1999). In green plants, the comparative study of gene families at the genome level revealed that the rate of gene gain and loss is about 0.001359 per gene per million years (Guo, 2013), which is similar to that in *Drosophila* (0.0012) and Mammalia (0.0016) (Demuth et al., 2006; Hahn et al., 2007). In particular, 2,745 to 2,928 core gene families were shared across green plants and regarded as the "core" proteome of green plants (Guo, 2013; Van Bel et al., 2012). Though many genes with redundant functions are eliminated after duplication, lots of them are retained. Retained genes could be divided into two categories: genes with functional divergence and genes with overlapped function related to gene dosage for selection of high expression level (Kuzmin et al., 2020) (Figure 2A). In addition, *de novo* gene birth increases the number of genes. Comparative studies among 63 genomes of green plants revealed that many *de novo* genes, including the *de novo* gene *QQS* involved in starch biosynthesis network (Li et al., 2009), originated from intergenic regions, and their higher methylation level and lower expression level contributed to their establishment in natural populations (Li et al., 2016) (Figure 2A).

In contrast to gene gain, gene loss through genomic structural variations or loss-of-function (LoF) mutations could play an important role in adaptation as well (Olson, 1999) (Figure 2A). Many gene loss events are correlated with phenotypic variations in plant architecture, adaptation to acidic soil, seed shattering, and attraction of pollinators (Amrad et al., 2016; Gujas et al., 2012; Wu et al., 2017b; Xu et al., 2019). Intriguingly, the essential genes estimated based on the lack of loss-of-function mutation in the natural populations of *Arabidopsis* (Xu et al., 2019) largely overlap with the "core" proteome that shows up across all the studied green plants (Guo, 2013). Of the 9,249 protein-coding genes (34.0% of all protein-coding genes in the Col-0 reference genome) that do not have any LoF variant within 1,071 studied accessions, 4,235 genes (45.8%) belong to the "core" proteomes (Figure 2B). Beyond the gene gain or loss, homoeologous exchange in allopolyploids could generate extensive phenotypic diversity (Wu et al., 2021).

Repeat sequences, especially TEs, constitute a large fraction of the genome sequences in diverse organisms, actively transposing in germ and somatic cells. TEs could produce novel genes or transcripts, provide regulatory elements and modulate gene expression, and generate genomic instability and rearrangements (Goerner-Potvin and Bourque, 2018; Wei and Cao, 2016; Wells and Feschotte, 2020), and thus could influence diverse phenotypic traits. For example, TEs frequently inserted around the gene of *FLOWERING LOCUS C* (*FLC*), one determinant gene of flowering time in *Arabidopsis* (Baduel et al., 2021; Quadrana et al., 2016) and its close relative *Capsella rubella*, reduced the expression level of *FLC* and promoted flowering through a TE insertion at the 3′ untranslated region (UTR) of *FLC* (Figure 2C), and affected its mRNA stability (Niu et al., 2019). Besides flowering time, the insertion of TEs can affect various phenotypes, such as fruit color (Domínguez et al., 2020) and drought tolerance (Mao et al., 2015). In particular, TEs could regulate gene expression through epigenetic regulation by RNA-directed DNA methylation pathway (RdDM) or affect the stability of transcripts, contributing to adaptation (Li et al., 2018b; Niu et al., 2019; Quadrana et al., 2016; Stuart et al., 2016). In contrast, TEs can act as promoters or enhancers of gene expression (Figure 2C). For example, in lettuce, a CACTA-like transposon was inserted into the first exon of *LsKN1* and promoted gene expression and leafy head development (Yu et al., 2020). In apples, a long-terminal repeat retrotransposon insertion at the upstream of *MdMYB1*, acting as an enhancer, contributed to the red fruit color (Zhang et al., 2019). TEs can also lead to exon shuffling, resulting in gene fusion or new genes (Cosby et al., 2021) (Figure 2C). The frequent insertion of TEs in *C. rubella* relative to its outcrossing sister species *Capsella grandiflora* contributed to its rapid phenotypic variation and rapid adaptation, although the former has a much lower genetic diversity, which demonstrated how a species with low genetic diversity can have higher adaptive ability, and to some extent, revealed the mystery of "genetic paradox of invasion" (Niu et al., 2019).

Besides TEs, other repeat sequences can regulate gene expression. In particular, STRs play a crucial role in gene regulation. For example, in *Arabidopsis*, the intronic GAA/TTC triplet expansion within the *IIL1* gene can reduce its expression through RdDM by accumulating 24-nt short interfering RNAs (siRNAs) and repressive histone marks (Eimer et al., 2018; Sureshkumar et al., 2009) (Figure 2C). In addition, correlation studies in natural *Arabidopsis* accessions reveal that length variations of STRs can affect gene expression and phenotypic variation (Press et al., 2018; Reinar et al., 2021).

Introgression between species and populations could contribute to adaptation. Frequent introgression events were observed in diverse species, contributing to genetic diversity, natural adaptation or domestication (Han et al., 2015; Kryvokhyzha et al., 2019; Zhou et al., 2020). In the *Capsella* genus, introgressions from its two ancestor diploid species are sources for adaptation of the allotetraploid *Capsella bursa-pastoris* (Han et al., 2015; Kryvokhyzha et al., 2019). In the genera *Triticum* and *Aegilops*, introgression of tetraploid wheat contributed to the unbalanced genomic diversity of different sub-genomes of the hexaploid bread wheat and provided new insights on crop breeding improvement (Zhou et al., 2020). Similar results in bread wheat were observed in

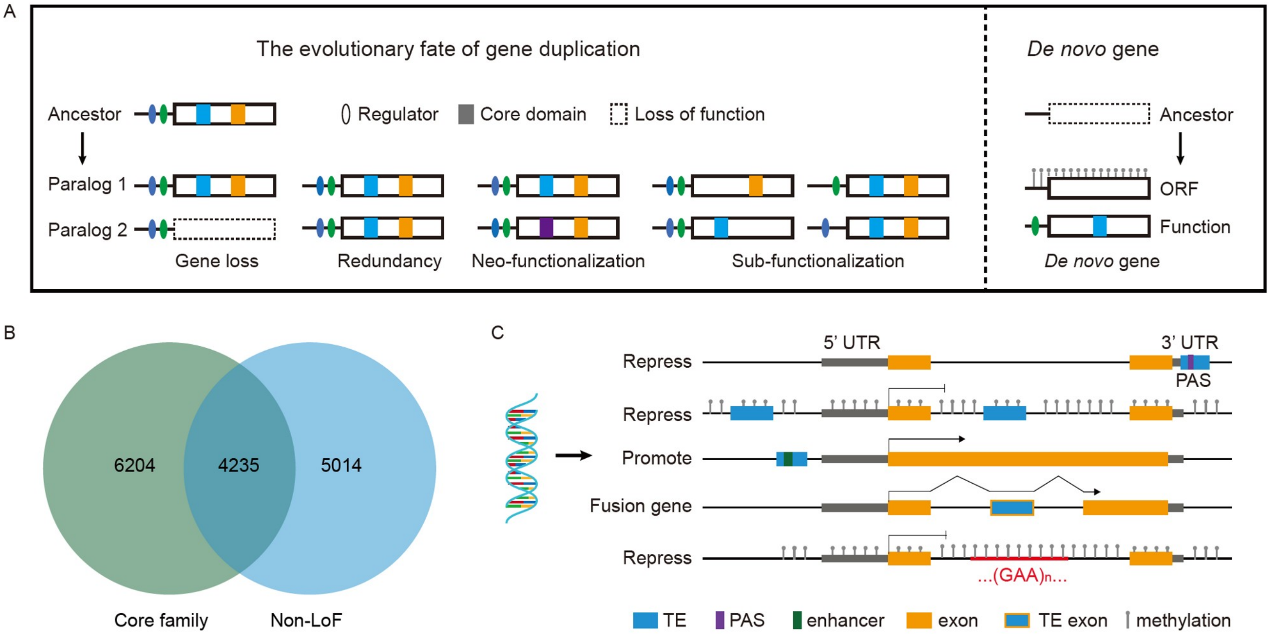

Figure 2 Gene copy number variation, essential genes, and structural variation are correlated with adaptation. A, Events changing gene copy number. Duplicated genes could be lost for redundant function, or both copies retained due to different causes, including the dosage balance effect, one copy may gain a new function through acquiring new regulatory or functional domains, or the two copies may have different functions through sub-functionalization. *De novo* genes usually have a high DNA methylation and low expression level at early stages; they could be maintained or spread in a population and will become functional after gaining regulatory elements or functional domains. ORF indicates an open reading frame. Colors indicate different regulators or core domain elements. B, The overlap of essential genes identified by the gene family study across green plants and gene loss-of-function study in natural populations of *Arabidopsis*. Core family indicates *Arabidopsis* genes within the shared core families in green plants. Non-LoF indicates genes without any loss-of-function in all natural *Arabidopsis* accessions. C, The effect of genetic variation of TEs and STRs. TEs inserted into 3' UTR regions induced alternative polyadenylation signal (PAS) and repressed gene expression by reducing RNA stability. TE insertion at the genic region could reduce gene expression levels via the RdDM pathway. TEs can provide enhancers or act as promoters and upregulate gene expression. TEs can act as exons and lead to gene fusion events. Polymorphism of STRs in the intron of genes can regulate gene expression by altering the level of DNA methylation.

the diploid and tetraploid progenitors of wheat (He et al., 2019; Przewieslik-Allen et al., 2021).

Adaptive evolution based on population genomics

Natural selection can contribute to plant adaptive evolution. Based on reads mapping to the reference genomes, population genomic studies of adaptive evolution are fruitful. Population genomics sequencing speeds up the study of adaptive evolution, such as the study of over 1,001 *Arabidopsis* genomes, transcriptomes and DNA methylomes (Cao et al., 2011; Clark et al., 2007; Durvasula et al., 2017; 1001 Genomes Consortium, 2016; Kawakatsu et al., 2016; Long et al., 2013; Zou et al., 2017), the study of the adaptation of maize landraces (Romero Navarro et al., 2017), sequencing of cultivated and wild rice (Huang et al., 2012; Wang et al., 2018; Xu et al., 2012), sequencing of the wild plant green millet (*Setaria viridis*) (Mamidi et al., 2020), the study of 1,506 wild sunflowers (Todesco et al., 2020), and over 2,898 genomic sequencing of soybean (Liu et al., 2020). Population genetic studies of *Arabidopsis* revealed that lots of genomic loci were under positive selection (Cao et al., 2011; Clark et al., 2007; 1001 Genomes Consortium, 2016; Long et al., 2013; Zou et al., 2017). Based on selective sweep scanning and genetic mapping, the flowering time gene *SVP* is important for the adaptation of *Arabidopsis* to a new habitat, the Yangtze River basin (Zou et al., 2017). In the living fossil plant, ginkgo, the sequencing of the worldwide natural populations revealed the evolutionary history of its extinction, competition, and adaptation (Zhao et al., 2019). In addition, population-based comparisons between closely related species contribute to our understanding of evolutionary biology, such as adaptation to desert habitats (Hu et al., 2021), convergent local adaptation (Yeaman et al., 2016), and parallel speciation (Cai et al., 2019).

Besides positive selection, balancing selection also contributes to adaptation. Balancing selection maintains advantageous genetic variation and contributes to adaptation. It is exemplified by the ABO blood group in primates (Ségurel et al., 2012), the major histocompatibility locus in vertebrates (Klein et al., 2007), leaf chemical profile genes in a perennial wildflower (Carley et al., 2021), disease resistance (R) genes (Karasov et al., 2014), and the self-incompatibility (S) loci (Guo et al., 2011; Nasrallah, 2002) in plants. It is important to identify genes that are under balancing selection across the whole-genome in different lineages, given those genes must correlate with adaptation. Comparative studies of genome-wide scanning analysis between *A. thaliana* and *C. rubella* reveal that many genes correlated with resistance to stress and fundamental functions are under balancing selection (Wu et al., 2017a). A similar study in the genus *Capsella* using two sister species revealed that long-term balancing selection was an important factor in shaping the genetics of immune systems (Koenig et al., 2019).

Long-read sequencing and *de novo* assembly of the pan-genome provide a great opportunity to study adaptive evolution. In soybean, the study of *de novo* assembly of 26 representative accessions reveals that non-reference SVs contributed to adaptive evolution, for example, a structural variation of a 1.4 kb indel in the promoter region of *SoyZH13_14G179600*, a Fe^{2+}/Zn^{2+} regulated the transporter gene, and contributed to the variation of Fe absorbing efficiency under different pH soils (Liu et al., 2020). In the tomato, long reads sequencing of 100 lines reveals that SVs can influence gene expression levels and further contribute to fruit flavor, size, and production, and the distribution of SVs along the genome can also reflect introgression during breeding and domestication (Alonge et al., 2020). In wheat, during modern wheat breeding, different haplotypes of *Sm1* mediated by SVs are associated with insect resistance (Walkowiak et al., 2020). In rice, a pan-genome study of 33 accessions revealed that *OsVIL1* gene CNVs result in delayed flowering and increased grain number in long-day conditions (Qin et al., 2021).

Adaptive evolution based on the association between sequence variation and climate parameters

Climate change could affect adaptive evolution, biodiversity, and global crop production (Lobell et al., 2011; Román-Palacios and Wiens, 2020). It is crucial to reveal how to protect species in the context of climate change. The adaptive evolution of plants reflects the results of natural populations' change and adaptation, or extinct along with climate change (Exposito-Alonso et al., 2019). Climate data are important in investigating the spatiotemporal divergence patterns for the large-scale study of flora and biodiversity protection (Chen et al., 2019; Jin et al., 2021; Lu et al., 2018). Species distribution modeling (SDMs), also known as ecological niche modeling, is a traditional approach to study the interplay of the distribution of a species and the environmental conditions and to predict the species' suitable habitat under changing climate (Elith and Leathwick, 2009). However, this approach does not consider the genetic background and evolutionary potential of a species (Aguirre-Liguori et al., 2021). Clustered SDMs first identify clusters or subspecies within a species, then build SDMs for separate clusters and improve the power of this method (Smith et al., 2019).

Owing to advances in sequencing technologies, it is now feasible to incorporate genomic data into ecological niche modeling, which can overcome the disadvantages of SDMs and detects genomic regions under adaptive evolution. The study of the association between species or populations with different genetic backgrounds and environmental data is an effective way to identify genomic regions under adaptive evolution. In *Arabidopsis*, the analysis of the association between the genotype and environmental data showed that many genetic loci are significantly correlated with ecological factors (Fournier-Level et al., 2011; Hancock et al., 2011; Shen et al., 2014; Xu et al., 2019). For example, based on the association between 517 natural *A. thaliana* lines and environmental variables, the results showed that manipulation of the amount of rainfall could affect the fitness, and many native *A. thaliana* populations are at an evolutionary risk (Exposito-Alonso et al., 2019). Similarly, association studies in teosinte indicate that inversions and intergenic variations are correlated to local adaptation (Pyhäjärvi et al., 2013). Besides the association approach, BayEnv and BayeScenv are two Bayesian methods to identify environmentally associated loci that are not affected by demography and genetic drift (Aguirre-Liguori et al., 2017; Evans et al., 2014). In addition, with the study of genetic response to different environmental factors, the pattern of phenotype dynamics and mechanistic interplay could be deeply understood, which plays an important role in developing strategies for species protection and agricultural production (Li et al., 2018a; Scheres and van der Putten, 2017).

To predict the fate of populations under climate change, gradient forest algorithms and generalized dissimilarity models are used to build non-linear models that associate identified candidate loci with specific environmental variables (Aguirre-Liguori et al., 2019; Gougherty et al., 2021; Waldvogel et al., 2020). With such models, one can calculate the expected genetic distance between the current population and the population that may have to face changed environments, which often is referred to as "genetic offset" (Fitzpatrick and Keller, 2015) or "genomic vulnerability" (Bay et al., 2018). The observed adaptive loci are the result of plants adapting to historical environments. However, in natural habitats, plant adaptation is extremely complex, with dynamic interactions across biotic, abiotic, and migration events (Soberón, 2010). Thus beyond the methods mentioned above, integrated approaches, which take into account the diverse factors, including gene flow, genetic offsets, genetic load, and dispersal, are necessary for the adaptive simulated analysis (Aguirre-Liguori et al., 2021). Therefore, with the present and predicted future environmental data, the adaptation potential of plants could be evaluated. The above studies provide insights into the conservation of endangered species and are also crucial for crop breeding for specific regions.

Adaptive evolution based on life history and functional traits

Many life histories and functional traits of plants, such as seed dormancy (Bentsink et al., 2010; Bewley, 1997), flowering time (Hepworth and Dean, 2015; Weigel, 2012), the speed of pollen tube growth (Zhong et al., 2019), the diversification of flowers and fruits (Shan et al., 2019; Wang et al., 2014; Yang et al., 2012), leaf shape (Chitwood and Sinha, 2016; Vlad et al., 2014), the balance between vegetative growth and disease resistance to microbial infection (Todesco et al., 2010), and stress tolerance (Chen et al., 2021; Hang et al., 2018; Kang et al., 2013; Ma et al., 2015; Zhang et al., 2022) are crucial for adaptation. To study the variation in these traits and their evolutionary genetic mechanisms is important in understanding plant adaptation. Here we only focused on a few traits as examples.

Seed dormancy, determining germination time at the proper environmental condition, is an adaptive trait and initiates the life cycle of plants. It is regulated by diverse factors, such as light, temperature and time of dry seed storage, levels of phytohormone such as gibberellin acid, abscisic acid (ABA), and brassinosteroid (BR) (Alonso-Blanco et al., 2009; Penfield, 2017). In particular, the gene *DELAY OF GERMINATION1* is an important gene that can regulate seed dormancy and germination (Bentsink et al., 2006; Bentsink et al., 2010). A recent study found that FLOE1, a prion-like protein functioning as a water potential sensor, could regulate seed germination through hydration-dependent phase separation as well (Dorone et al., 2021). It is interesting that the *COOLAIR* can not only regulate flowering time but also controls seed dormancy in response to temperature changes (Chen and Penfield, 2018).

Flowering time, a key link in the transition of plants from vegetative growth to reproduction, is a representative life history trait and model system to understand adaptation. In *Arabidopsis*, hundreds of genes are correlated with flowering time, including two determinant genes, *FLC FRI* (*FRIGIDA*) and (*FLOWERING LOCUS C*). The flowering time gene *FRI* could explain over 70% of the natural variation of flowering time (Hepworth and Dean, 2015; Weigel, 2012). Besides the sequence variations of *FRI* and *FLC*, the noncoding antisense transcript of *FLC*, the *COLD INDUCED LONG ANTISENSE INTRAGENIC RNA* (*COOLAIR*), can repress the expression of *FLC* by histone demethylation (Liu et al., 2010). In addition, other genes, for example, the variations of the *SVP* gene, contribute to the flowering time variation of natural *Arabidopsis* in the Yangtze River basin (Zou et al., 2017). In contrast to *Arabidopsis*, in its closely related species, *C. rubella*, the genetic variation of *FLC* regulated its natural variation of flowering time to a large extent (Guo et al., 2012; Niu et al., 2019; Yang et al., 2018). In detail, two overlapping deletions in the 5′ UTR of *CrFLC* influenced the local changes in chromatin conformation and histone modifications and reduced its expression (Yang et al., 2018). The variation at the 3′ UTR of *FLC*, which is influenced by TE insertion, reduced *FLC*'s expression (Niu et al., 2019) (Figure 2C). A single nucleotide mutation at the end of the last intron induced the alternative splicing and produced weak *FLC* (Guo et al., 2012). Overall, genetic variation of the *FLC* gene regulates the flowering time in natural populations of *C. rubella*, unlike in *Arabidopsis*, in which flowering time is largely regulated by the natural variation of the *FRI* gene. In summary, specific genes or even their specific regions are hotspots of mutation to regulate phenotypic variation, implying that, to some extent, evolution is predictable.

The morphological pattern of flowers, fruits, and cuticles are important traits for plant adaptation. In *Nigella damascene*, *LATE MERISTEM IDENTITY1* contributes to the lateral organ diversification of short trichomes and bifurcation of the lower lip (Zhang et al., 2020a). In the Tanunculaceae, the non-expression/down-regulation of *APETALA3-3* contributes to the parallel losses of petals (Duan et al., 2021). In *Primulina heterotricha*, the persistently asymmetric expression of two *CYCLOIDEA2* genes leads to the origins of floral zygomorphy, which contribute to plant-insect coevolution and the adaptive radiation of angiosperms (Yang et al., 2012). CNVs of repeat sequences in the intron of *Physalis Organ Size 1* lead to flower and fruit size variation of tomatillo (*Physalis philadelphica*) (Wang et al., 2014). By identifying a critical transcription factor controlling cuticle formation in the early-diverging land plant *Marchantia polymorpha*, it has been demonstrated that the cuticle genetic network has evolved by a stepwise process, and the evolution of land plant-specific MIXTA-lineage MYB transcriptions have led to the origin of the plant cuticle, a key innovation that has contributed to the plant terrestrialization (Xu et al., 2021a).

Insights into molecular mechanisms and challenges of adaptive evolution study

Phenotypic traits are the most obvious patterns reflecting adaptation to environments by animals and plants. Adaptive traits have been described for centuries; however, the discovery of their underlying mechanisms lagged far behind due to technical or methodological limitations. Owing to the high throughput sequencing and multi-omics development, mechanism dissection of adaptive traits progressed rapidly in recent decades. Through comparative genomics and population genomics, candidate genes could be discovered at the genome-scale, facilitating our understanding of adaptive traits controlled by multiple genes, which appears more and more common. Except for the role of coding sequences, the importance of regulatory elements has been demonstrated, as shown in a wide range from beak morphology in classic Darwin's finches (Yusuf et al., 2020) to social behavior in laboratory mice (Wang et al., 2020). Facilitated by advances in methodology and techniques, high resolution study of functional traits has become possible. For instance, post-transcriptional and post-translational modifications were identified in hibernation adaptation, as mentioned above

(Andrews, 2019; Grabek et al., 2015). In addition, the CRISPR/Cas9 system provides a powerful tool to verify gene function contributing to functional traits and has been widely used in studies of traits including but not limited to cancer research (Hart et al., 2015; Slipek et al., 2019), crop improvement (Zhang et al., 2021), biotechnology, and many more (Adli, 2018). Overall, we are in a great era to understand the underlying mechanisms of adaptive traits.

Besides the above constitutive genetic makeups, the role of other factors in functional traits is emerging. Counterintuitively, gene loss events are thought to contribute to mammalian and plant adaptations (Sharma et al., 2018, Xu et al., 2019). Pseudogenes play a role in aquatic adaptation in cetaceans to avoid harmful diving effects (Huelsmann et al., 2019) and in subterranean adaptations in naked mole-rats and blind mole-rats to prevent hypoxic damage (Zheng et al., 2022), opening another window for us to understand the complexity of adaptation. Gut symbionts recycled nitrogen from urea in the hibernating thirteen-lined ground squirrels, and the nitrogen was then incorporated again by the squirrels, preventing them from protein imbalance, which is a great challenge for hibernators because of the lack of dietary nitrogen (Regan et al., 2022). These new data further extend our knowledge of the basis of adaptive traits and call for deeper and wider investigations in future studies.

Nevertheless, there are some challenges in studying adaptive evolution. Firstly, it is a challenge to accurately measuring the phenotype of traits that could reflect the changeable natural environments. Secondly, the limited computational ability and theoretical models and algorithms are insufficient to handle big data. For example, a recent study in *Arabidopsis* reveals that mutations are not randomly produced in the genome; particularly, the mutation rate is reduced in functionally constrained regions, which is largely correlated with epigenetic modification (Monroe et al., 2022). Thirdly, more comprehensive studies involving diverse methods, such as evolutionary biology, molecular genetics, and biochemistry, are needed to validate the variation of a certain trait or sequence variation that is correlated to adaptive evolution. Overall, the study of adaptive evolution is theoretically and practically important in biodiversity conservation, domestic animal and plant breeding and human health, and more in-depth studies are urgently needed in this area.

Convergent evolution in wild animals and plants

The term convergent evolution refers to the phenomenon in which, during evolution, species with distant evolutionary relationships produce similar phenotypes with the same or similar functions in response to the same living environment or selective pressure (Losos, 2011; Stern, 2013; Storz, 2016). Convergent evolution is important evidence for the adaptation of species to the environment (Grant et al., 2004; Hoy, 2012). The study of convergence evolution can help understand the adaptive mechanisms and survival strategies of species and assist in exploring the predictability and repeatability of biological evolution (Losos, 2011; Stern, 2013; Storz, 2016). In addition to the identification and description of phenotype convergence, investigating the evolution of morphological or molecular convergence can effectively link genotypes and phenotypes, which has increasingly become a topical issue in evolutionary biology (Mahler et al., 2017; Stern, 2013).

Convergent evolution of wild animals

Owing to the rapid development of high throughput sequencing technology, it has become a research priority to examine the evolutionary mechanisms of molecular convergence using large-scale data and multi-omics analysis methods. The concept of molecular convergence has also expanded from convergence of amino acid substitutions in coding genes to gene loss convergence, expression regulation and pattern convergence, and gut microbiome convergence (Doolittle, 1994; Rosenblum et al., 2014). Recently, substantial numbers of studies on convergent evolution and molecular convergence in animals have been reported in the context of survival behaviors, focusing mainly on communication, extreme environment adaptation, and predation (Figure 3).

Echolocation convergence

The echolocation system is a very special type of auditory mechanism. By detecting high-frequency sound waves reflected by objects, animals can accomplish positioning, navigation, predation and other behaviors in environments with poor light, which play an important role in animal survival and reproduction (Jones and Holderied, 2007). In mammals, echolocation systems occur mainly in Cetartiodactyla (whales and even-toed ungulates) and Chiroptera (bats) (Dallos and Fakler, 2002). These two groups diverged 90 million years ago and independently evolved echolocation systems (Jones and Holderied, 2007), making them a classical model for studying convergent evolution.

Earlier molecular studies identified a “star” gene related to echolocation, namely, the *Prestin* gene. It encodes a type of motor protein that is expressed in the outer hair cells of the cochlea and is significantly related to high-frequency hearing (Dallos and Fakler, 2002). In the mammalian Prestin protein tree, the echolocating bats and toothed whales are grouped together instead of clustering with their respective closely related species (Li et al., 2010; Liu et al., 2014). Further analyses of convergent substitution sites and functional validation identified a convergent substitution (N7T) in *Prestin*

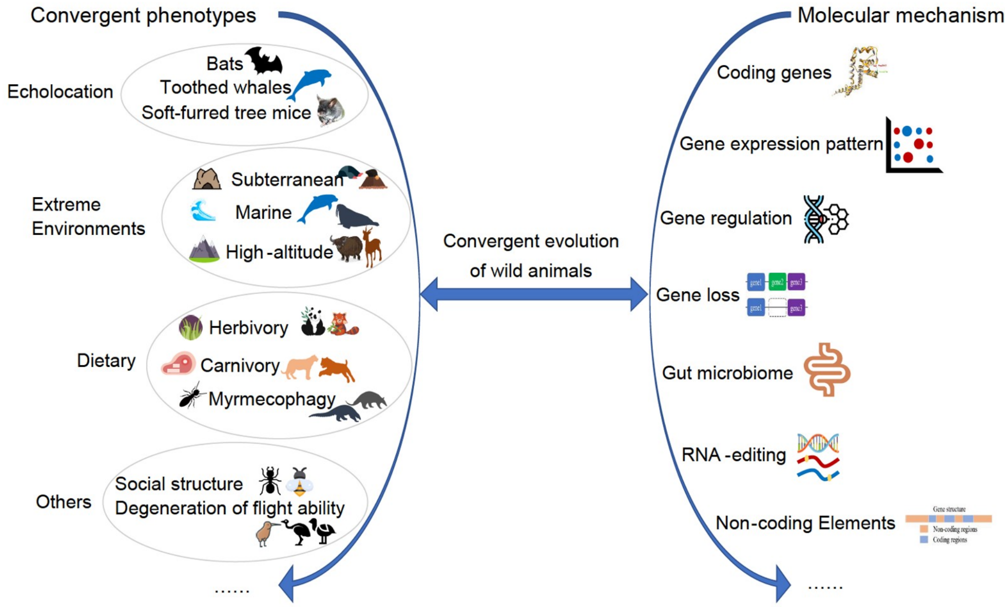

Figure 3 Schematic illustration of the convergent evolution studies of wild animals

in echolocating bats and toothed whales accounting for the functional convergence of response to high-frequency sound waves (Li et al., 2010; Liu et al., 2014). Parker et al. (2013) first analyzed the molecular mechanism of convergent echolocation at the genomic level and found convergent amino acid substitutions of about 200 genes (including *Prestin*) in echolocating bats and dolphins, most of these genes being related to auditory and visual phenotypes (Parker et al., 2013). Lee et al. (2018) recovered convergent amino acid substitutions in three additional high-frequency hearing-related genes (*STRC*, *TECTA*, and *CABP2*) and four skeletal muscle fiber-related genes (*CASQ1*, *ATP2A1*, *MYH2*, and *MYL1*) in echolocating bats and dolphins, based on comparative genomic analyses of 30 mammals. In addition, the expression levels of four skeletal muscle fiber genes, which are associated with vocal organ functions, in echolocating mammals are significantly higher than those in non-echolocating mammals. In particular, the calcium storage protein calsequestrin 1 (CASQ1) in bats and dolphins is able to form calcium-sequestering polymers at lower calcium concentrations than in non-echolocating mammals (Lee et al., 2018).

However, Thomas and Hahn (2015) detected more convergent genes between bats and cattle (the sister groups of dolphins) than between bats and dolphins, and only 19 genes overlapped with the convergent genes identified by Parker et al. (2013) (Thomas and Hahn, 2015), a result which was subsequently supported by Zou and Zhang who observed that the probability of the same amino acid substitutions in distant evolutionary lineages was much lower than that in close evolutionary lineages due to random substitutions (Zou and Zhang, 2015a; Zou and Zhang, 2015b; Zou and Zhang, 2017). In addition, Rey et al. (2018) proposed that the comparison of the site-wise log-likelihood support (ΔSSLS) method used by Parker et al. (2013) to screen for convergent substitutions uses criteria that are relatively laxer than those of other methods, thus leading to false positive results. It has therefore been proposed that multiple methods for the detection of convergent amino acid substitutions should be used in combination in order to obtain more reliable results (Zhou et al., 2015).

In addition to functional amino acid substitutions, Davies et al. (2014) compared the rates of evolution of conserved noncoding elements (CNEs) between echolocating mammals (bats and dolphins) and non-echolocating mammals. They found that CNE substitution rates are significantly higher in echolocating mammals than in non-echolocating mammals, and interestingly, among them, the rapidly evolved CNEs correspond to the *Hmx2* and *Hmx3* genes, which are associated with auditory system development and hearing and may have contributed to the convergent evolution of echolocation (Davies et al., 2014).

The molecular mechanisms of the communication system in convergent echolocation between bats and toothed whales not only provide new concepts for connecting genotype and adaptive phenotype but also facilitate exploring the extent of predictability and repeatability in the process of the evolution of echolocation. He et al. (2021) combined behavioral, anatomical, genomic, and functional experiments to confirm the echolocation behavior of soft-furred tree mice, a mammalian species that has evolved echolocation traits independently from the known echolocating species (bats and toothed whales). Soft-furred tree mice have the same anatomical features in terms of vocal and auditory structure as those in echolocating bats and are also significantly enriched in genes related to auditory functions convergently with the bats and toothed whales, including the widely studied echolocation-related gene *Prestin*. Further functional experiments have demonstrated that the functional convergence of the *Prestin* gene is driven by convergent amino acid substitutions in the soft-furred tree mice and other echolocating species (He et al., 2021). These findings extend our knowledge of the convergent evolution of echolocation traits to rodents, providing a remarkable example of evolutionary predictability and repeatability.

Convergence in adaptation to extreme environments

(1) High-altitude environments

As mentioned above, high-altitude environments characterized by low oxygen, low temperature, and high ultraviolet radiation represent one of the most extreme challenges for animal survival. Different animals living in high-altitude regions have evolved convergent phenotypes to adapt to such a harsh environment, including increased lung capacity, the ability to deliver oxygen to body tissue (Gerald et al., 2003; Schaller, 1998), hemoglobin (Hb)-O_2 affinity, and metabolic capacity (Beall, 2000; Monge and Leon-Velarde, 1991; Wu and Kayser, 2006).

Many indigenous wild mammals on the Qinghai-Tibet Plateau show convergent evolution of adaptation mechanisms. For instance, Tibetan antelope and plateau pika share seven positively selected genes related to DNA repair and ATPase production (*ADORA2A*, *CCL2*, *ENG*, *PIK3C2A*, *PKLR*, *ATP12A*, and *NOS3*), revealing the mechanism of adaptation of these two plateau species to hypoxia and the high level of ultraviolet radiation in the environment (Ge et al., 2013). Wang et al. (2015) found that genes related to energy metabolism, low-temperature response, and ultraviolet protection had undergone accelerated evolution in both Tibetan antelope and yak genomes and that the *SOCS4* gene, which is related to the blood oxygen system, showed significant convergent evolution between these two species. Three snub-nosed monkey species (the black snub-nosed monkey, the golden snub-nosed monkey, and the Myanmar snub-nosed monkey) occurring in the high-altitude southwestern region to the east of the Qinghai-Tibet Plateau share eight amino acid substitutions in six genes (*CDT1*, *RNASE4*, *ARMC2*, *NT5DC1*, *RTEL1*, and *DNAH11*) related to lung function, DNA repair, and angiogenesis compared to the other snub-nosed monkeys (the gray snub-nosed monkey and the Tonkin snub-nosed monkey), which live in low-altitude regions (Yu et al., 2016). Further functional assays confirmed that the mutant type *CDT1* (537V) renders cells more resistant to ultraviolet radiation than the wild-type *CDT1* (537A), and the mutant type *RNASE4* (89K and 128I) confers a more enhanced ability to induce endothelial tube formation *in vitro* than the wild-type *RNASE4* (89N and 128T) (Yu et al., 2016).

In addition, Zhang et al. (2016) examined whether there is convergent evolution of mammalian gut microbes during high-altitude environmental adaptation. They found that the fermentation products of the rumen microbiome of the Qinghai-Tibet Plateau ruminants (Tibetan sheep and yak) included higher proportions of volatile fatty acids (energy-supplying substances produced by the fermentation of the microbiome) than those of low-altitude cattle and sheep. Further metagenomic analyses of rumen microbiome clustered the microbiota structures of these two high-altitude ruminants together, and their rumen microbiomes were both significantly enriched in the pathway for volatile fatty acid synthesis and metabolism, suggesting convergent adaptation in the composition and function of rumen microbiomes in plateau ruminants. This study shows that in addition to the convergent evolution of the host genome, the convergent evolution of the symbiotic microbiome is also a mechanism for mammalian adaptation to plateau conditions, providing a new perspective on the evolution of animal adaptation (Zhang et al., 2016).

Studies of convergent evolution of high-altitude adaptation in non-mammals have gradually begun to increase our understanding of convergent evolution. Zhu et al. (2018) discovered that two convergent amino acid substitutions in the hemoglobin protein, which is encoded by the *HB* gene (A34T and P119A), in passerine birds from distantly related genera (*Parus* and *Lophophanes*) and families (Aegithalidae and Anatidae) native to the Qinghai-Tibet Plateau, are responsible for the increase in Hb-O_2 affinity and the affinity-enhancing effects in *HB* observed in these high-altitude passerine birds. Besides the convergence of functional amino acid substitutions, Hao et al. (2019) found that the tissue expression profiles of three independently evolved high-altitude passerine birds are clustered together separately from their low-altitude relatives, suggesting that convergent changes in gene expression have also occurred in response to high-altitude environmental stress. Sun et al. (2018) performed a comparative genomic analysis to detect convergent genes related to plateau adaptation in lizards and frogs. They did not find convergent amino acid substitutions but recovered convergent changes at the functional level with significant functional enrichment in oxidative stress and hypoxia response pathways, indicating that convergent evolution can also occur at the functional level, albeit without convergent amino acid substitutions.

(2) Subterranean environments

The subterranean environment is characterized by low oxygen, high carbon dioxide, and the absence of light. Subterranean species generally show increased red blood corpuscle counts and contents of hemoglobin and myoglobin, as well as the absence of pinnae and reduced eyes (Dubost, 1968; Wei and Ma, 2001; Wei et al., 2006; Zeng et al., 1984).

By analyzing gene expression levels in subterranean zokors and naked mole rats, Deng et al. (2014) identified 20 upregulated genes that are related to heart function, red blood cell function, aerobic respiration, and musculoskeletal function in both subterranean rodents. The gene expression profile analyses clustered these two subterranean rodents together and apart from their relatives. Based on comparative genomic analyses of the subterranean pikas and zokors, Shao et al. (2015) identified 787 functional genes with convergent amino acid substitutions, which were enriched in ATPase activity, blood vessel development, and respiratory gaseous exchange.

In comparison, Davies et al. (2018) performed genomic analyses of four independently evolved subterranean groups (mole-rats, golden moles, spalacids, and star-nosed moles) and found that convergent amino acid substitutions were enriched mainly in genes seemingly unrelated to high-altitude adaptation, including craniofacial and kidney development, sperm development and immune response whereas shared positively selected genes were enriched mainly in hypoxia-related pathways, such as angiogenesis, hearing, smell, and skin elasticity. Accordingly, the authors proposed that different mammals adapted to the subterranean environment through the adaptive selection of genes rather than through convergent amino acid replacement (Davies et al., 2018).

In addition, Partha et al. (2017) detected 55 functional genes that had undergone accelerated evolution and are highly enriched in eye and skin development processes in all of these four subterranean groups, indicating that the subterranean environment has driven the relaxation of selective pressure on these genes and resulted in a convergent phenotype related to vision loss and skin degradation (Partha et al., 2017). Furthermore, Roscito et al. (2018) showed that the enhancer region of the eye development-related gene *PAX6* has an accelerated evolutionary rate, and this affects the regulation of *PAX6* gene expression and lens development. The excessive accumulation of mutations is thus closely related to the convergent phenotype of visual loss (Roscito et al., 2018).

(3) Marine environments

The aquatic environment constitutes a completely different ecological niche from the terrestrial environment. Distantly related marine mammals, including cetaceans (whales and dolphins), sirenians (manatees and dugongs) and pinnipeds (seals, sea lions and walruses), evolved independently from different land ancestors but developed similar morphological characters, physiological functions, and ecological habits to adapt to the marine environment, including a streamlined body shape with modified limbs, the dense limb bone for walking underwater, and reduced oxygen consumption for adaptation to hypoxia (Foote et al., 2015; McGowen et al., 2014).

Foote et al. (2015) analyzed 20 mammalian genomes and found that 44 genes had convergent amino acid substitutions in these three marine mammalian groups, of which eight genes (*MYH7B*, *TBC1D15*, *MGP*, *SMPX*, *GCLC*, *SERPINC1*, *M6PR*, and *S100A9*) were also positively selected and related mainly to bone formation, hyperthyroidism, myocardial formation, and regulation of coagulation. The functions of these genes are closely related to adaptation to the marine environment (Foote et al., 2015). In the same year, Zhou et al. (2015) conducted a comparative genomic analysis on 62 mammals and found that 26 convergent genes are unique to the three marine mammalian groups. These genes are associated with muscle contraction, vascular contraction regulation, fatty acid oxidation, and skin development (Zhou et al., 2015). Chikina et al. (2016) analyzed 59 mammals and detected about 560 accelerated evolution genes that are related to the sensory system, muscle function, skin and connective tissue, lung function, and lipid metabolism. The newly developed "Convergence at Conservation Sites (CCS)" method reduces random convergence at rapidly evolving sites and falsely inferred convergence caused by erroneous inferences of the ancestral character (Xu et al., 2017). Yuan et al. (2021) further found that three genes (*FAM20B*, *NFIA*, and *KYAT1*) show convergent amino acid substitutions in the three marine mammal lineages, which are associated with their blubber development and musculoskeletal system to adapt to the marine environment (Yuan et al., 2021).

Dietary convergence

Dietary habits are an important connecting link between animals and their environment. Dietary modification in animals, therefore, plays an important role in their adaptation to the environment. Animals with the same dietary habits show convergent characteristics in physiological structures, digestive mechanisms, and microbial composition of the digestive tract (Karasov and Douglas, 2013).

(1) Herbivory convergence

The most classic study of convergent dietary evolution is the research on the molecular mechanism of herbivory convergence in the giant panda and the red panda. The two pandas belong to different families of Carnivora and diverged about 43 million years ago (Eizirik et al., 2010). They both experienced drastic changes from carnivorous to omnivorous, then herbivorous diet, and evolved the same habit of obligately feeding on bamboo, which has a low nutritional value and high fiber content (Schaller et al., 1986). To adapt to this unique dietary habit, both pandas have evolved pseudo-thumbs in order to grasp bamboo easily (Antón et al., 2006). Hu et al. (2017) detected convergent amino acid substitutions in 70 genes enriched in protein digestion and absorption, retinol metabolism, appendage development, and cellular component assembly, which are associated with the development of pseudo-thumb and the absorption and utilization of essential nutrients from bamboo. In particular, *DYNC2H1* (R3128K and K3999R) and *PCNT* (S2327P and Q2458R) are two genes involved in limb development through cell ciliary structure assembly (Dagoneau et al., 2009; Endoh-Yamagami et al., 2010; Merrill et al., 2009), and might be important in regulating the development of the pseudo-thumb in pandas. In addition, ten pseudogenes are shared by the two pandas, including pseudogenization of the umami receptor gene *Tas1r1* (Hu et al., 2017). Umami is a critical taste sense in meat-eating animals that enables them to perceive components of meat and other protein-rich foods, so the pseudogenization of the gene may have been an evolutionary response to the dietary shift from carnivory to herbivory. This study reveals the adaptive molecular mechanisms underlying the convergence of morphological traits (such as the pseudo-thumb) and physiological traits (such as the utilization of essential nutrients from the specialized food source, bamboo) at multiple levels, including convergent amino acid substitutions, metabolic pathways and pseudogenes, providing a benchmarking example of research on convergent evolution.

In addition, Huang et al. (2021) compared the composition, structure and function of gut microbiota between the two pandas and their carnivorous relatives and found that the pandas shared more similarities in their gut microbiota structure with one another than with their relatives. Moreover, key enzymes involved in the VB12 biosynthesis pathway that are related to the bamboo-feeding habit adaptation have been identified in both pandas (Huang et al., 2021). Interestingly, three convergent substitutions (M212L, D406K, and H407D) in the *GIF* gene, whose product is essential in VB12 absorption, have undergone positive selection in the genomic analyses of both pandas (Hu et al., 2017), suggesting that the convergent evolution of host genomes and that of symbiotic microbiomes, as well as host-microbiota coevolution, are important driving forces in the dietary adaptation of animals.

(2) Carnivory convergence

Contrary to the dietary switch of the two pandas from carnivory to herbivory, many marine mammals have undergone a dietary switch from herbivory to carnivory (Pauly et al., 1998). Wang et al. (2016) found convergent amino acid substitutions in the proteinase gene *CTRC* (I4V) and in the lipase genes *CYP7A1* (R190K and N208H) and *PNLIP* (I69L) in carnivorous cetaceans and terrestrial carnivores, suggesting that carnivorous mammals have convergently evolved the ability to digest proteins and lipids to adapt to their diets (e.g., high-protein and high-lipid fishes and invertebrates) (Wang et al., 2016). By sampling more carnivorous species, Kim et al. (2016) found a unique convergent amino acid substitution (A269V) in the *EMB* gene in all carnivorous species compared to herbivorous and omnivorous species. This gene affects the growth of motor neurons and neuromuscular connections (Lain et al., 2009), which may be related to the predatory behavior of carnivores (Kim et al., 2016). In addition to the convergent amino acid substitutions, they also discovered a significant contraction of the UDP-glucuronosyltransferase (UGT) gene family, which is involved in the detoxification of plant-derived toxins in all carnivorous species. This contraction is likely to be related to the lack of plants in the diet of carnivorous mammals (Kim et al., 2016).

Interestingly, convergent gene loss has also been recorded in studies of molecular convergence during the evolution of carnivory. Meyer et al. (2018) found that the Paraoxonase (*PON1*) gene has been lost across all independently evolved marine mammals compared to terrestrial mammals. This convergent functional loss of *PON1* is likely related to the decrease of omega-6 polyunsaturated fatty acids in the diet of marine mammals (Meyer et al., 2018). Besides the marine mammals, Hecker et al. (2019) also found that 44 genes, including the umami taste receptor genes *TAS1R1*and *TAS1R2*, the sour taste receptor gene *PKD2L1*, and the detoxification gene *UGT1A6*, were convergently lost in five independently evolved carnivorous mammals (Hecker et al., 2019). The loss of these genes has been reported to be related to the carnivorous habits of mammals (Feng et al., 2014; Jiang et al., 2012). Four additional genes related to dietary habits were lost in these carnivorous animals. They included *INSL5* and *RXFP4*, which control appetite and maintain blood glucose levels (Grosse et al., 2014), *NR1I*3, whose product reduces plant-derived xenobiotics (Hecker et al., 2019), and *NOX1*, which is an innate immune system gene (Kawahara et al., 2004). The loss-of-function of these four genes is related to the dietary composition and irregular eating behavior of carnivorous mammals.

(3) Myrmecophagy convergence

Development of highly specialized myrmecophagy (ant and termite-eating) across different mammalian orders (echidnas, numbats, anteaters, pangolins, armadillos, aardvarks, and aardwolves) is one of the most spectacular events in mammalian evolution. Delsuc et al. (2014) characterized the convergence of microbial composition and diversity in myrmecophagous mammals using 16S rRNA. They found that the microbial compositions of myrmecophagous mammals are clustered together, suggesting convergence of the gut microbiota in these specialized myrmecophagous animals (Delsuc et al., 2014).

Convergent evolution of wild plants

Convergent evolution of phenotypic similarities among species is also prevalent in the plant kingdom. Driven by the adaptation to similar environments, many phenotypic convergences, such as pollinator attraction, parasitism, carnivorousness, C_4/CAM photosynthesis, salt gland, specialized leaves, and aerial roots, have evolved from independent clades (Christin et al., 2010; Xu et al., 2017; Xu et al., 2020). Although complex genetics of these convergent phenotypes would suggest many possible molecular paths to the same solution, the repeated hitting on the same genetic changes indicates the predictability of plant molecular evolution. Recently, the detections of genomic convergence among plants inhabiting the same habitats effectively indicate adaptive evolution in plants and extend the molecular convergence from amino acid substitutions to CNVs, expression alterations, and other tissue-level genetic changes (Xu et al., 2020). This section summarizes the advances in the understanding of convergent evolution in wild plants, including the adaptation to abiotic and biotic stresses, innovation of morphological traits, and specialized metabolite production (Table 1). We further discuss the extent and coexistence of molecular convergence at different tissue levels and emphasize the influence of frequently occurred WGDs that distinguished plant genomes from animal genomes. We also note that empirical and theoretical studies of genomic convergence in plants are still limited and put forward key scientific questions to be addressed.

Abiotic stress tolerance

Many types of extreme environments on the earth confer abiotic stresses, such as high salinity, flooding, desiccation, low temperature, high temperature, low nutrient availability, or a combination of at least two of these. During independent adaptation to desiccation, eight desiccation-tolerant plants convergently gained an average of 20.7 early light-induced proteins (ELIPs) per genome by tandem duplication, compared to 3.1 per genome in 66 desiccation-sensitive plants (Van Buren et al., 2019). These tandemly duplicated ELIPs have 622-fold higher expression in desiccation-tolerant than desiccation-sensitive plants under water-deficient conditions, protecting against photo-oxidative damage to photosynthesis organelles during prolonged dehydration. Conversely, continuous water logging is another abiotic stress for land plants. During the long-term adaptation to aquatic environments of two independent seagrass lineages, *Halophila* and *Zosteraceae*, many conserved monocot core genes associated with ethylene and terpenoid biosynthesis have been convergently lost (Lee et al., 2018).

High salinity is a significant stress for plants in the desert, coastal, marine, and other saline soil environments. This results in osmotic stress, which reduces water uptake, and ion toxicity due to the accumulation of toxic ions such as Na^+ (Gong et al., 2020; Zhang et al., 2020). Salt-tolerant plants (halophytes) have independently evolved in 37 of the 65 plant orders (Bennett et al., 2013; Cheeseman, 2015; Flowers et al., 2010). For example, the high-affinity K^+ transporter 1 (*HKT1*) gene copy number convergently increased in two halophytes, *Thellungiella salsuginea* and *Populus euphratica*, through tandem duplication (Ma et al., 2013; Wu et al., 2012). *HKT1* promotes Na^+ retrieval from the xylem, reducing Na^+ accumulation in shoots (Busoms et al., 2018; Gong et al., 2020). Dramatic increases in duplicated copy gene expression confer high salinity tolerance to these plants.

Cold or freezing is a common stressor for plants living at high altitudes. Zhang et al. (2019) identified many convergent amino acid substitutions in two distantly related Antarctic psychrophilic green algae. Genes involved in photosynthesis, multiple antioxidant systems, and translation are overrepresented among loci with convergent amino acid substitutions. The lodgepole pine (*Pinus contorta*) and interior spruce (*Picea glauca*, *P. engelmannii*, and their hybrids) that diverged ~140 million years ago evolved a pattern of local adaptation to the climate that reflects a tradeoff between competition for light resources and the acquisition of freezing tolerance. By searching for correlations between individual SNPs and environmental variables in individuals from >250 populations of the two clades, Yeaman et al. (2016) identified 47 genes with SNPs associated with spatial variation in temperature or cold hardiness in both species.

Intertidal zones, which are interfaces between land and sea, are among the most extreme environments for plants. These regions exhibit multiple abiotic stressors, such as high and fluctuating salinity, hypoxia, low nutrient availability, and strong UV radiation. Furthermore, these conditions fluctuate temporally and spatially (Duke, 1992; Feng et al., 2021; He et al., 2022; Nguyen et al., 2015; Tomlinson, 1986). More than 400 genes from high-quality whole genomes of three mangroves (*Avicennia marina*, *Rhizophora apiculate*, and *Sonneratia alba*, independently originating from inland ancestors) experienced convergent amino acid substitutions (Xu et al., 2017). These convergent genes are enriched in salt tolerance and seed development pathways, which may be essential for mangrove adaptation. The intertidal zone's highly stressful and fluctuating environmental conditions have also driven the convergent evolution of whole genomes. Lyu et al. (2018) found that three major mangrove clades have massively reduced TE loads by reducing transposon generation rates. In a stressful and fluctuating environment, TE loss may be a convergent strategy employed by mangroves to maintain genome stability. The three mangrove clades also experienced convergent amino acid alterations, underusing amino acids with large hydrophobic residues that are harmful to protein stability and overusing amino acids with low energy costs (He et al., 2020).

Biotic stress tolerance

Biotic stress is the recurrent attack on plants by pests, parasites, or microbial pathogens. Three independent lineages of ash trees (in the genus *Fraxinus*) evolved resistance to

Table 1 Multiple modes of molecular convergence in plants. The examples marked with an asterisk are from Xu et al. (2020).

Plant taxa	Phenotype	Type of molecular convergence				References
		Amino acid substitutions	Gene copy number	Gene expression	Whole-genomic composition	
Eight desiccation-tolerant plants*	Resurrection from dehydration	–	Tandem duplication of *ELIPs*	High expression of *ELIPs* under water-deficit conditions	–	(Van Buren et al., 2019)
Thellungiella salsuginea and *Populus euphratica**	High salinity tolerance	–	Tandem duplication of *HKT1*	–	–	(Wu et al., 2012; Ma et al., 2013)
C4 lineages in Cyperaceae, grass, and eudicot*	C4 photosynthesis	*PEPC*, *rbcL*		–	–	(Besnard et al., 2009; Christin et al., 2007; Christin et al., 2008)
Ananas comosus, *Phalaenopsis equestris* and *Kalanchoe fedtschenkoi**	CAM photosynthesis	*PEPC*, *HY5* and two CAZyme genes	*PEPC* and *PPCK*	54 genes	–	(Yang et al., 2017)
Cephalotus follicularis, *Drosera adelae*, *D. muscipula* and *Nepenthes alata**	Carnivorousness	GH19 chitinases, purple acid phosphatases and RNase T2s	–	*AMT1*	–	(Fukushima et al., 2017)
Three mangrove clades: Rhizophoreae, *Avicennia* and *Sonneratia**	Viviparous seeds, aerial roots, high tannin content, high salinity tolerance	~400 genes	–	–	Amino acid composition change; TE content reduction	(Xu et al., 2017; Lyu et al., 2018; He et al., 2020)
Parasitic species of Orobanchaceae*	Parasitism	*KAI2d*	*KAI2d* is a rapid-evolving clade of *KAI2* duplication	–	–	(Conn et al., 2015)
Cuscuta campestris and Parasitic species of Orobanchaceae	Parasitism	–	18 independent horizontal gene transfer (HGT) events	12 HGTs are haustorial expressions	–	(Yang et al., 2019)
Striga, *Cuscuta* and *Sapria*	Parasitism	–	convergent loss of genes involving photosynthesis, defense, and stress response	–	–	(Cai et al., 2021)
Lennoaceae, Hydnoraceae, Cynomoriaceae, Apodanthaceae, Cytinaceae, and Orobanchaceae	Parasitism	–	Massive gene loss of plastome	–	–	(Schneider et al., 2018)
Halophila and Zosteraceae*	Adaptation to the aquatic environment	–	Loss of conserved genes	–	–	(Lee et al., 2018)
Antarctic psychrophilic green algae*	Freezing tolerance	54 genes	–	–	–	(Zhang et al., 2019)
lodgepole pine (*Pinus contorta*) and interior spruce (*Picea*)*	Cold environment tolerance	47 genes	–	–	–	(Yeaman et al., 2016)
Arabidopsis thaliana	Loss of vernalization	–	Loss of *FRIGIDA* gene	–	–	(Shindo et al., 2005)
ash trees (genus *Fraxinus*)*	Resistance to emerald ash borer (*Agrilus planipennis*)	53 genes	–	–	–	(Kelly et al., 2020)
Soybean and *A. thaliana*	Resistance to pathogen *Pseudomonas syringae*	–	Recruit R genes *RPM1* and *Rpg1-b*	–	–	(Ashfield et al., 2004)
Coffee, cacao and tea	Caffeine biosynthesis	–	Tandem duplication of *NMTs*	–	–	(Denoeud et al., 2014)
Pinus sylvestris, *Arachis hypogaea* and *Vitis vinifera*	Stilbene biosynthesis	–	Stilbene synthase duplicated from chalcone synthase	–	–	(Tropf et al., 1994)
Boraginaceae, monocots, and Asteraceae family	pyrrolizidine alkaloid biosynthesis	–	homospermidine synthases duplicated from deoxyhypusine synthase	–	–	(Reimann et al., 2004)
Four independent clades of Andean Iochrominae	losses of pigment delphinidin			Loss of gene expression: *F3′5′H*, *DFR* and *ANS*		(Larter et al., 2018)
Oryza, *Echinochloa* and *Calohypnum plumiforme*	Momilactone biosynthesis	–	Recruit duplicated genes to form a biosynthetic gene cluster	–	–	(Mao et al., 2020)

the emerald ash borer (*Agrilus planipennis*, EAB). A whole-genome study found that 53 genes underpin the evolution of resistance, most containing convergent amino acid substitutions with independent origins (Kelly et al., 2020). These candidate genes are involved in herbivore recognition, defense signaling, programmed cell death, and phenylpropanoid biosynthesis, which generates products closely related to disease and insect resistance. Thus, these convergent genes may play critical roles in the independent evolution of EAB resistance.

Phylogenetically unrelated plant disease resistance (*R*) genes have independently evolved to mediate the recognition of the same pathogens. For example, the *R* genes from soybean, *Rpg1-b*, and *A. thaliana*, *RPM1*, are distantly related but have convergently acquired the ability to recognize the same type III effector protein from the pathogen *Pseudomonas syringae* (Ashfield et al., 2004). Convergent evolution of plant innate immune system receptors has also been observed in *A. thaliana*, apple, and barley (Carter et al., 2018; Prokchorchik et al., 2020).

Morphological traits

As plants from different lineages adapt to the same environmental conditions, they often evolve specialized morphological traits independently. Convergent molecular changes drive many adaptations. The independent development of C_4 and Crassulacean acid metabolism (CAM) in C_3 photosynthesis is one of the most significant innovations. These alternative modes of photosynthesis have evolved in diverse plant species more than 60 times. CAM and C4 mechanisms increase photosynthesis efficiency by concentrating carbon temporally or spatially and help plants grow under hot and dry conditions (Heyduk et al., 2019). The phosphoenolpyruvate carboxylase (*PEPC*) and *rbcL* genes encode vital enzymes for CO_2 fixation and have experienced many convergent amino acid substitutions across C_4 lineages. *PEPC* has 21 convergent sites among eight grass C_4 lineages and 16 convergent sites in five lineages of the second most species-rich C_4 family, Cyperaceae (Besnard et al., 2009; Christin et al., 2007). The gene *rbcL* has eight convergent sites in 23 monocot C_4 lineages (Christin et al., 2008). Yang et al. (2017) identified convergent amino acid substitutions in four genes and convergent expression changes in 54 genes in three CAM plant genomes. These convergent amino acid substitutions may increase PEPC activity. Significant time shifts in *diel* transcript expression may be related to nocturnal CO_2 fixation, circadian rhythms, carbohydrate metabolism, stomatal movement, and heat stress responses.

Carnivory is a significant phenotypic innovation that has evolved in more than 600 plant species (Adamec, 1997; Thorogood et al., 2018). Carnivorous plants have developed highly specialized leaf-derived pitfall traps to attract, trap, and digest small animals and absorb the released nutrients. Fukushima et al. (2017) found that four carnivorous plants repeatedly co-opted stress response genes to enable digestive physiology. Repeatedly utilized proteins (GH19 chitinases, purple acid phosphatases, and RNase T2s) accumulated convergent amino acid substitutions. These convergent amino acid substitutions tend to be located at exposed positions of digestive enzymes and may be selected by insect-derived substrates, high endogenous proteolytic activity, and low pH.

Parasitic plants that obtain carbon and other nutrients from their host plants have evolved in multiple plant lineages. Parasitic plants have modified roots (haustoria) and degenerated organs. Many studies have found that the evolutionary acquisition of plant parasitism is highly consistent, including convergent gene loss, horizontal gene transfer (HGT), and amino acid substitutions. The *D14* gene and the duplicated gene *KAI2d* mediate host detection in parasitic plants. More copies of *KAI2* are found in ten Orobanchaceae parasite genomes than in non-parasitic Lamiales species. Furthermore, additional *KAI2d* copies accumulated excess amino acid substitutions, causing protein structural changes and strigolactone recognition (Conn et al., 2015). Compared to an autotrophic relative *Tiquilia plicata*, the plastids of two parasitic Lennoaceae plants (*Lennoa madreporoides* and *Pholisma arenarium*) are 50% smaller (Schneider et al., 2018). Most plastid genes involved in photosynthesis have been convergently lost. *Cuscuta campestris* and Orobanchaceae share 18 HGT events from their hosts (Yang et al., 2019). These genes are highly expressed in haustorial tissues, suggesting they contribute to metabolism and parasitic ability in these two parasitic lineages. In the genomes of three parasitic lineages, *Sapria*, *Cuscuta*, and *Striga*, 642 genes associated with photosynthesis, defense, and stress responses were lost (Cai et al., 2021).

Plant specialized metabolites

Specialized metabolism attracts other organisms beneficial to plants or defends against other biotic and abiotic stresses (Chen et al., 2019). Independent evolution of making the same compounds has been detected in many plant lineages (Pichersky and Lewinsohn, 2011). For example, caffeine is synthesized in independent coffee, cacao, and tea lineages. Genomic analyses have found that caffeine *N*-methyltransferases (NMTs) convergently expanded through tandem duplications in these species (Denoeud et al., 2014). Stilbenes associated with defense against fungal diseases are synthesized via the key enzyme stilbene synthase (STS). Evolutionary analyses found that STSs arose independently multiple times in different plant lineages from chalcone synthase (Tropf et al., 1994). Homospermidine synthase (HSS) catalyzes the first specific step of pyrrolizidine alkaloid production. Many plants produce these compounds as a defense against herbivores. HSS has independently been recruited from the ubiquitous enzyme deoxyhypusine synthase (DHS) at least four times during angiosperm evolution (Reimann et al., 2004). In 28 species of the Andean clade Iochrominae, four independent losses of the pigment delphinidin involved convergent loss of the expression of three genes (*F3'5'H*, *DFR*, and *ANS*) (Larter et al., 2018). Momilactones are bioactive diterpenoids that contribute to defense against pathogens and allelopathic interactions between plants. The biosynthetic gene cluster that produces momilactones independently evolved in *Oryza*, *Echinochloa*, and *Calohypnum plumiforme* (Mao et al., 2020).

Modes of convergent evolution in plant genomes

Repeated evolution of the same set of genetic solutions may indicate the presence of strong constraints on the possible responses to environmental stresses. Mutation bias, probability, the magnitude of beneficial mutations at a specific locus, and pleiotropic effects on non-targeted protein functions influence the possibility of convergent evolution (Stern, 2013). The drive to minimize pleiotropic effects and simultaneously maximize adaptation can result in molecular convergence (Stern, 2013). Convergent amino acid substitution, the most widely observed molecular convergence, is rarely detected, especially at the whole-genome level. Cis-regulatory regions having fewer pleiotropic consequences than protein-coding regions are hot spots of convergent molecular evolution (Stern, 2013). Since the fitness effects of amino acid mutations are often conditional on the genetic background, the probability of convergence decreases as the possibility of acceptable beneficial mutations decreases as sequences diverge (Storz, 2016). At the whole-genome level, many convergence events are neutral. These can easily overshadow the few actual instances of adaptive convergent evolution (Goldstein et al., 2015; Rokas and Carroll, 2008; Xu et al., 2017).

Extensive high-quality genomic data allow us to move beyond studying convergent amino acid substitutions to including gene duplication, gene loss, expression alterations, and even whole-genome composition changes (Shindo et al., 2005). From the cases described above, multiple molecular modes of convergent evolution can co-occur. The evolution of C_4 and CAM plants has been observed at the level of single genes and whole genomes, amino acid substitutions, expression profiles, and CNVs (Yang et al., 2017). In parasitic plants, the convergent evolution of host recognition gene sequences, gene loss, and HGT has promoted host coexistence. The *ELIP1* gene has experienced both convergent copy number expansion and expression alteration in resurrection plants. During adaptation to intertidal environments, mangrove genomes convergently evolved amino acid substitutions, amino acid composition, and TE content (He et al., 2020; He et al., 2022; Lyu et al., 2018). Gene copy number changes, such as gene duplication, gene loss, and HGT, are common in plants, probably because of high gene duplication and loss rates. Multi-level genome convergence strongly indicates the prevalence of molecular convergence during plant adaptive evolution.

Molecular convergence and WGDs

One of the most significant genomic differences between plants and other organisms is the many duplicated genes on plant genomes, including small-scale and large-scale duplications, up to WGDs. WGDs are particularly common in plants compared to other taxa (Van de Peer et al., 2017; Wu et al., 2019). WGDs have convergently occurred during extreme environmental perturbations in many independent plant lineages. For example, convergent WGDs have been observed in at least 22 angiosperm clades during the drastic environmental changes during the Cretaceous-Paleogene (K-Pg) boundary (Ren et al., 2018; Vanneste et al., 2014; Van de Peer et al., 2017; Zhang et al., 2020). A more recent convergent WGD event was observed in the grass Andropogoneae. A minimum of 34 distinct polyploidy events may have promoted the dominance of C_4 over C_3 grasses (Estep et al., 2014). Although whether polyploidy is easily triggered by environmental stress or is a common stress adaptation is still debated, the high survival rate of plant lineages that experience paleopolyploidy and the high-stress tolerance of polyploids indicate the adaptive role of these WGDs. The convergent retention and loss of gene duplications produced by WGD have also been observed in multiple plant lineages. Gene families involved in conditional responses to biotic and abiotic stress are more likely to maintain multi-copy genes, indicating the convergent role of WGDs during environmental adaptation (Li et al., 2016; Van de Peer et al., 2017).

The abundant genetic material provided by WGDs in different lineages has convergently evolved. For example, critical genes in the cold-response and shade avoidance pathways were convergently retained after eight independent WGD events at the K-Pg boundary (Wu et al., 2019). Expression divergence of the *ICE1* and *ICE2* duplicated genes indicates their role in cold tolerance. Convergent evolution of novel expression profiles after WGD under fluctuating salt concentrations has been found in the mangrove plants *R. apiculata* and *A. marina* (Xu et al., 2021b). Many convergent expression alterations and amino acid substitutions of C_4/CAM-related genes are due to gene duplication. While convergent retention of C_4-related genes has been found, whether WGDs have produced them requires additional exploration (Emms et al., 2016; Yang et al., 2017).

Methods for detecting molecular convergence

Neutral evolution and positive selection can produce convergent genetic changes. In both simulation and empirical data, many neutral convergent amino acid substitutions have been observed, especially at the whole-genome level (Foote et al., 2015; Thomas and Hahn, 2015; Xu et al., 2017; Zou and Zhang, 2015a). Therefore, distinguishing adaptive from neutral convergent events is the primary consideration for method development.

Zhang and Kumar (1997) developed statistical tests to examine whether the observed numbers of convergent changes could be explained by random chance. The test was used to identify the convergent evolution of stomach lysozyme sequences in foregut fermenters. However, the influence of random convergence is magnified at the whole-genome level. Neutral amino acid substitutions significantly influence background noise and thus the inferred expected random convergence using this approach (Zou and Zhang, 2015b). Therefore, when detecting convergence using the whole proteome, the number of adaptively convergent sites may be higher or lower than the expected neutral convergence, depending on the neutral model used.

The site-specific likelihood support (SSLS) approach calculates SSLS values for a null hypothesis of the species tree (H_0) and an alternative hypothesis of a convergence tree (H_1). The difference in the SSLS between H0 and H1 (ΔSSLS) is calculated for each site. This approach was developed to detect convergence between snakes and agamid lizards at 13 mitochondrial genes (Castoe et al., 2009). It was then extended by Parker et al. (2013) to the whole-genome level. However, it was criticized for lacking suitable controls (Thomas and Hahn, 2015; Zou and Zhang, 2015a). To eliminate random convergent events in whole genomes, Xu et al. (2017) developed the approach of detecting such events at conservative sites (CCS). This method first identifies CCS by restricting the control groups and the outgroup to the same state and detecting convergent amino acid substitutions at CCS. It also sets a symmetric phylogeny between focal and control groups and uses convergent site counts in the control group to estimate random convergence. Rey et al. (2018) searched for convergent shifts in amino acid preferences instead of convergent substitutions to the same amino acid. CNEs may function as regulatory sites and play roles in adaptive evolution. Hu et al. (2019) proposed a Bayesian method to model substitution rate changes in conserved elements across a phylogeny. That approach revealed numerous examples of CNEs with accelerations specific to phenotypically convergent lineages.

Additionally, studies have found that not all convergent phenotypes result from loci subject to convergent evolution. Some ancestral polymorphic loci result from incomplete lineage sorting, which may also be the molecular mechanism of convergent phenotypes (Li et al., 2017) and can lead to incorrect interpretations of phenotypic evolutionary history, especially in lineages that experienced speciation events in rapid succession (Feng et al., 2022). Therefore, distinguishing between molecular mechanisms when inferring convergent evolution in different species should receive more attention, especially in species experiencing adaptive radiation.

Detecting molecular convergence in whole genomes remains a major challenge, and approaches that maximally eliminate random or false convergence and retain true adaptive convergence are urgently needed. In particular, the number of duplicated genes in plant genomes is significantly higher than that in other organisms. Since the role of gene duplications in plant adaptive evolution is widely acknowledged, the development of molecular convergence detection approaches that consider gene duplication should be useful in studying genetic convergence.

Insights from convergent evolution studies

In the genomic era, studies on convergent molecular evolution are no longer limited to comparing known candidate genes or small numbers of genes. More data types can be studied, such as the sequences of different genomic regions (both coding and noncoding regulatory regions), temporal and spatial differences in gene expression (transcriptomics), and gut microbiota co-evolving with the host (metagenomics). Through comparative multi-omics methods, evidence for molecular convergence related to specific traits can be examined on a finer scale and in unprecedented detail, providing information from the convergence of commonly observed amino acid substitutions in genes to gene loss, gene regulation, gene expression patterns, copy number variation, and microbial composition. Beyond these, post-transcriptional convergence, such as the A-to-I RNA editing that contributes to the caste differentiation system in honeybees and flies (Duan et al., 2021), and the convergence of post-transcriptional gene regulatory pathways between distinct species via species-specific *Alu* short interspersed element (SINE) insertions in primates and rodents have also been reported recently (Lucas et al., 2018; Maquat, 2020). Furthermore, with the development of epigenetic technologies such as Hi-C, ChIP-seq, and ATAC-seq, convergent evolution research is expected to make breakthroughs in exploring epigenetics-mediated convergence.

Besides well-known systems for investigating convergent evolution, as summarized above, an increasing number of convergent traits have been identified, described, and studied. For example, Pan et al. (2019) and Sackton et al. (2019) found that convergent amino acid substitutions and accelerated conserved non-exonic elements (CNEEs) contributed to the convergent loss or degeneration of flight ability during avian evolution. Berens et al. (2015) and Qiu et al. (2018) found that social insects, including ants and bees, with the same hierarchical systems, have experienced convergent evolution in gene regulatory networks. Yang et al.

(2021) found that similar gene expression profiles and convergent nutrient metabolism pathways are associated with common group-living behaviors of independently evolved spiders.

More and more phenotypic changes resulting from various types of molecular convergence have been verified at the cellular and organism levels, which has benefited from the rapid development of gene-editing technologies such as CRISPR/Cas9. These technologies greatly facilitate the functional validation of convergent mutations and provide important evidence for the critical step from molecular convergence to phenotypic convergence. For example, Karageorgi et al. (2019) performed CRISPR/Cas9 editing to confirm the cardiac glycoside specialization function of three convergent amino acid substitutions in *ATPα* genes identified in molecular analyses of convergent evolution in monarch butterflies (Agrawal et al., 2012; Dobler et al., 2012; Holzinger et al., 1992; Petschenka et al., 2013; Petschenka et al., 2017; Zhen et al., 2012). These butterflies have independently evolved to colonize plants that produce cardiac glycoside toxins (Karageorgi et al., 2019). Additional examples may be discovered in the future, increasing our understanding of convergent evolution.

Coevolution

Populations of two or more species may interact and exert reciprocal selective effects on traits, and the traits of each species may evolve in response to traits of the other, which is called coevolution (Janzen, 1980). Coevolution is classified as mutualistic and antagonistic according to the interaction relationship between the two partners. Mutualistic coevolution includes mutualism, such as coevolution between a host and symbiont microorganisms, and antagonistic coevolution includes parasitism, predation, and competition (Futuyma, 2013). Long-term coevolution could result in coadaptation between the species.

Wild animal-related coevolution

For a long time, understanding genetic mechanisms underlying animal-related coevolution depended on studies of model animals such as *Drosophila* and *Caenorhabditis elegans*. Some coevolution cases have revealed single-gene or major-effect gene mechanisms in wild animals. However, multi-gene or genome-wide mechanisms are relatively rarely reported. Here, we summarize the research advances of molecular mechanisms underlying wild animal-related coevolution based on the interaction type (Figure 4).

Mutualism

Application of next-generation sequencing technology has revealed that the gut microbiota in humans and animals have played active roles in the host's nutrient utilization, health, and disease (Ezenwa et al., 2012; Morgan et al., 2013). Thus, coevolution between the host and gut microbiota is considered mutualistic coevolution. Co-speciation is an important evolutionary outcome of coevolution systems of host and gut microbiota, i.e., a pattern of cophylogeny for both hosts and their gut microbiota. Moeller et al. (2016) found that multiple lineages of the predominant bacterial taxa in the gut, such as clades of Bacteroidaceae and Bifidobacteriaceae, arose through co-speciation with hominids over the past 15 million years. Furthermore, Gaulke et al. (2018) used eco-phylogenetics to identify conserved gut bacteria and found that cophylogeny between mammalian orders and their gut microbiomes occurred within the Bacteroidales. Youngblut et al. (2019) investigated the coevolution between different vertebrate groups and their gut microbiomes and found that Mammalia had a stronger cophylogeny signal than non-mammals. These findings suggest that, compared with other vertebrate groups, co-speciation has occurred between mammals and some gut microbiota.

Metagenomics provides in-depth insights into the coevolution between wild animals and gut microbiomes at the molecular level. In the giant panda, for example, Zhu et al. (2011) used *16S* rRNA gene sequencing and metagenomics technologies to sequence their gut microbiota. They uncovered several kinds of *Clostridium* that degraded cellulose and identified the genes encoding cellulose-digesting enzymes. Giant pandas feed mainly on bamboo leaves or shoots in different seasons, which has resulted in changes in the gut microbiome to adapt to crude fiber digestion during the nutrient-deficient leaf period and to crude protein utilization during the protein-rich shoot period (Wu et al., 2017). Furthermore, the fecal microbiota transplantation of diet-specific feces from the giant pandas into a germ-free mouse showed that the butyrate-producing bacterium *Clostridium butyricum* was more abundant during the shoot-feeding season than the leaf-feeding season, and butyrate extended the upregulation of the hepatic circadian gene *Per2*, subsequently increasing phospholipid biosynthesis for utilization by giant pandas (Huang et al., 2022).

Hosts with endosymbionts are another important system of mutualistic coevolution. Uncovering the genetic mechanisms of coevolution provides deep insights into the formation of mutualism systems. McCutcheon and von Dohlen (2011) studied an interesting mutualism system: the mealybug *Planococcus citri* and dual bacterial symbionts (*Candidatus* Moranella endobia living inside the betaproteobacteria *Candidatus* Tremblaya princeps). There was little overlap in retained genes involved in nutrient production between the symbionts, and several essential amino acid pathways in the mealybug assemblage required a patchwork of interspersed gene products from Tremblaya, Moranella, and possibly *P.*

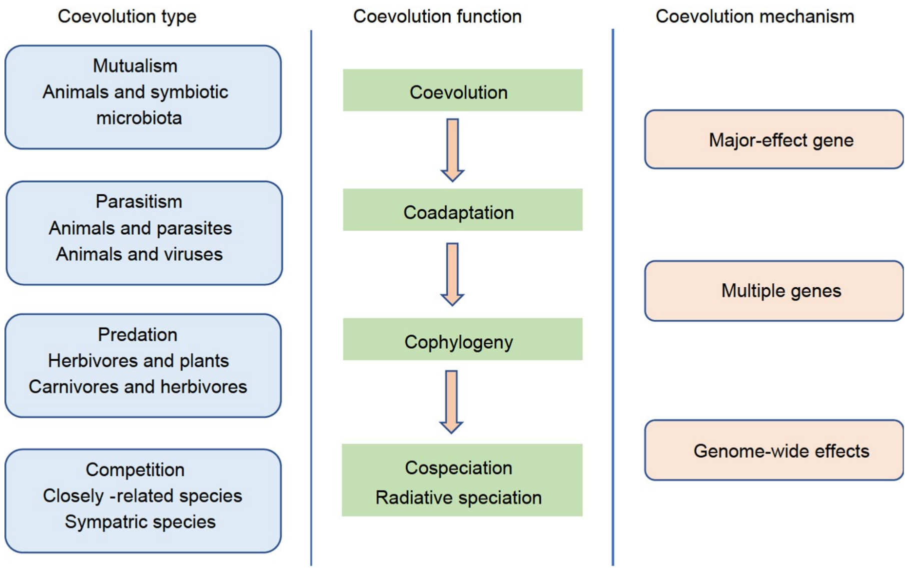

Figure 4 Schematic illustration of wild animal-related coevolution types and their functions and molecular mechanisms. Coevolution often results in coadaptation of both sides and, under some circumstances, results in cophylogeny, co-speciation, or radiative speciation.

citri, suggesting an interdependence for nutrient metabolism. Furthermore, comparative genomics found that at least 22 expressed horizontally transferred genes from multiple diverse bacteria into the mealybug genome likely complemented these missing symbiont genes, and the three-way symbiosis depended on genes from at least six lineages of organisms (Husnik et al., 2013).

Parasitism

Parasitism is a widespread type of coevolution in nature, such as animal hosts and parasites (on the body surface or *in vivo*) and brood parasitism. Co-speciation is often reported as a result of parasitism coevolution, for example, between pocket gophers and chewing lice, pigeons/doves and feather lice, and lizards and *Schellackia* parasites (Hafner and Nadler, 1990; Megía-Palma et al., 2018). Furthermore, Clayton et al. (2003) explored the factors driving coadaptation between pigeons/doves and feather lice and found that host defenses, i.e., preening in pigeons/doves, reinforced co-speciation by preventing the lice from switching between hosts of different sizes.

Some progress has been made in understanding molecular mechanisms underlying parasitism coevolution. A classic molecular mechanism is the resistance of host major histocompatibility complex (MHC) genes to parasites. De Bellocq et al. (2008) performed a meta-analysis and revealed that helminth species richness in rodent species was associated with increased MHC class II polymorphisms. Phillips et al. (2018) tested the resistance of guppies to a common ectoparasite and found that hosts carrying novel MHC variants experienced a 35%–37% reduction in infection intensity. Bento et al. (2017) explored the genetic basis of coevolution between the planktonic crustacean *Daphnia magna* and the bacterial pathogen *Pasteuria ramosa* and found that in natural populations, *Pasteuria* resistance locus polymorphisms were associated with variation in resistance, supporting the hypothesis of matching-allele interactions.

Furthermore, multi-gene or genome-wide coevolution mechanisms have been found in model animals. Gravato-Nobre et al. (2005) investigated the coevolution of *C. elegans* and its pathogen *Microbacterium nematophilum* and detected 121 mutants that altered the response to infection in *C. elegans*, suggesting that multiple genes are involved in coevolution. Cogni et al. (2016) observed multi-gene coevolution in *Drosophila melanogaster* resistance to the sigma virus and Drosophila C virus (DCV). For DCV resistance, two large-effect genes were primarily responsible for the variation in resistance, whereas sigma virus resistance involved five genes, which explained less than half the genetic variance. With the rapid development of genomics technology, genome-wide coevolution mechanisms have been explored in model animals. Papkou et al. (2019) used the coevolution system of *C. elegans* and its pathogen *Bacillus thuringiensis* to study the genomic basis of Red Queen coevolution dynamics and found that bacterial coadaptation was driven by copy number variation of a toxin-encoding plasmid, whereas host coadaptation was related to large genomic regions on multiple chromosomes, suggesting a complex genetic basis for the coadaptation.

Recently, the genomic basis of the coevolution between non-model animals and parasites was also explored. Using association mapping, Bourgeois et al. (2017) investigated the coevolution between *D. magna* and the bacterial pathogen *P. ramosa* and identified two genomic regions involved in resistance to *P. ramosa* under positive selection. Hu et al. (2021a) investigated the genomic mechanisms of coevolution between non-model mammals (giant panda, red panda, tiger, pig, and dog) and their respective parasitic roundworms and found that the CTSZ and P4HB immunoregulatory proteins played a central role in their protein interactions. Furthermore, seven pairs of interactive proteins showed gene-level coevolution, and these proteins were involved in the immune response. Additionally, Hu et al. (2021b) hypothesized that endosymbiosis systems were widespread among marine organisms, especially the unicellular photosymbiotic algae and multiple marine hosts, and the molecular mechanisms underlying these coevolution systems should be investigated with "omics techniques".

On the other hand, genome-level studies provide deep insights into the genetic mechanisms of parasite adaptation to parasitic life (Kirkness et al., 2010; Pan et al., 2013). These studies indirectly reflect the consequences of coevolution from the perspective of parasites. Kirkness et al. (2010) found that the genomes of the body louse and its primary bacterial endosymbiont *Candidatus* Riesia pediculicola reduced in size compared with their free-living close relatives. Furthermore, they found that the body louse genome contained significantly fewer genes associated with environmental sensing and response compared with other insect genomes, while the plasmid of *Candidatus* Riesia pediculicola harbored a unique arrangement of genes required for the synthesis of pantothenate, an essential vitamin deficient in the louse diet, representing a complex system of both parasitism and mutualism. Pan et al. (2013) performed comparative genomics of parasitic silkworm microsporidia and uncovered that the parasitic genomes expand through several common molecular mechanisms such as gene duplication, HGT, and TEs expansion, suggesting the potential roles of these molecular mechanisms in the adaptation to parasitism.

Predation

Studies of predation coevolution have mainly focused on the dynamic model and ecological progress of coevolution (Wilson et al., 2018; Yoshida et al., 2003), and single-gene molecular mechanisms were identified for some coevolutionary predation systems. A classic example is the coevolution between resistance in garter snakes and neurotoxin (TTX) in newt prey (Feldman et al., 2009; Feldman et al., 2010). Studies found that the garter snake had mutations in a voltage-gated sodium channel gene ($Na_v1.4$) to resist TTX. The mutation in $Na_v1.4$ correlated almost perfectly with TTX resistance in *Thamnophis sirtalis* and explained 23% of the variation in TTX resistance in *T. atratus* (Feldman et al., 2010). In squirrel prey resistant to rattlesnake venom, phenotype matching (e.g., living at similar elevations) played a role in the coevolution between venom metalloproteinase activity and the resistance effectiveness of prey (Holding et al., 2016).

Competition

Competition among species or populations often results in the separation of ecological niches and character displacement for adapting to unique niches, i.e., phenotypic diversification (Medina and Langmore, 2015; Schluter, 2010). Occasionally, coevolutionary competition results in radiative speciation; for instance, Darwin's finches inhabiting the Galapagos archipelago (Grant and Abbott, 1980) and Hawai'ian honeycreepers on the Hawaiian Islands. These two groups of birds are classic examples of adaptive radiative speciation. They both live on isolated islands and compete for limited food resources. As a result, differentiation of diet niches has occurred, producing fruit-eaters, insect-eaters, and seed-eaters. Furthermore, these birds evolved different beak morphologies adapted to special diets (Futuyma, 2013). The molecular bases of these phenotypic diversifications are often research hotspots. For the beak morphology of Darwin's finches, insights into the molecular basis developed from single genes to multiple genes and genome-scale effects (Abzhanov et al., 2004; Almén et al., 2016; Chaves et al., 2016; Lamichhaney et al., 2015; Lamichhaney et al., 2016; Lawson and Petren, 2017; Yusuf et al., 2020). For example, Abzhanov et al. (2004) found that the expression of *Bmp4* in the mesenchyme of the upper beaks strongly correlated with a deep and broad beak morphology. Lamichhaney et al. (2015) re-sequenced the genomes of 120 individuals representing all Darwin's finch species and found that a haplotype, including *ALX1*, encoding a transcription factor affecting craniofacial development, was strongly associated with beak shape diversity. Using GWAS analysis, Chaves et al. (2016) identified six SNPs that explained over 80% of the variation in beak size, suggesting that multiple genes might be responsible for beak size variation. Yusuf et al. (2020) identified 1,434 protein-coding genes and 39,806 noncoding regions possibly related to beak shape evolution and suggested that regulatory region changes were major drivers of morphological diversification over macroevolutionary timescales. These findings show that the genetic architecture underlying phenotype diversification is complex, and the genetic basis is often at the level of genome-scale effects.

Wild plant-related coevolution

Recent research progresses in the coevolution between wild plants, and their interacting organisms are reviewed below in four themes illustrating several study models (Figure 5). As a coevolution concept was proposed for plant-herbivore interactions (Figure 5A), molecular mechanisms of plant interaction with both mutualistic pollinators and antagonistic herbivores are discussed in those studies involving three preconditions for the coevolutionary relationships (Tong and Huang, 2019). Here, we follow that the interactive species would have involved reciprocal selection from each other

(Ehrlich and Raven, 1964) if evidence for ecological interactions, co-divergence, or cophylogeny and coadaptation is satisfied (Tong and Huang, 2019).

Mutualism

(1) Figs and fig wasps

The interaction between plants and pollinators has long been regarded as mutualism, while figs and fig wasps are one of the most rigid symbiotic relationships in nature (Machado et al., 2005; Weiblen, 2002; Yang and Wang, 2020). The interaction between figs and fig wasps is considered one-to-one species-specific mutualism, as around 750 *Ficus* species are pollinated by one or very few fig wasp species (Cook and Rasplus, 2003; Herre et al., 2008). In these symbioses (Figure 5B), the fig provides nutrition for the wasp larvae and reproductive sites for wasps, while fig wasps provide pollination for the figs (Cook and West, 2005; Janzen, 1979; Weiblen, 2002).

Three recent genomic studies have advanced our understanding of the molecular interactions between figs and fig wasps. Zhang et al. (2021) sequenced whole genomes of two *Ficus* species and one fig wasp species. They identified SNPs in 14 re-sequenced fig species (subgenus *Sycomorus*) and their corresponding pollinator species (*Ceratosolen*) to investigate the molecular mechanism of coevolution. Testing the coadaptation between wasp body size and fig fruit size, they found that 7 of 37 candidate genes (18.9%) related to fruit development and 14 of 62 wasp genes (22.5%) governing organ size were under purifying selection. In three fig wasp species pairs, they identified species-specific signaling compounds in floral scents, including isoprene-derived and benzenoid-derived components, in which synthesized pathways of chemical signal-related genes were under strong negative or purifying selection to enrich for terpenoid metabolite-related functions. In the wasp pollinator genome, genes encoding olfactory and gustatory receptor proteins of chemical cues had selective sweep signals (Zhang et al., 2021). That study was the first to unveil genomic evidence of purifying selection for phenotypic and chemical coadaptation between plants and pollinators.

To understand the molecular mechanism of the chemical interactions between figs and fig wasps, Wang et al. (2021b) assembled high-quality genomes of *Ficus pumila* var. *pumila* and its specific pollinating wasp *Wiebesia pumilae*. Their genomic analyses identified several genes regulating the specific temporal biosynthesis of pollinator attractants and validated their functions. A highly reduced number of odorant-binding protein genes was observed in the pollinator, and an odorant-binding protein mainly bound the plant-synthesized attractant. They found similar secondary metabolites associated with chemical defenses throughout the development of galled ovules and seeds. This, combined with the significant reduction in detoxification-related gene families in the wasp, may have shaped the specialized detoxification ability to form highly specific pollinator-host symbioses. In a phylogenomic study in the fig wasp system, Wang et al. (2021a) sequenced the nuclear, chloroplast, and mitochondria genomes from 15 representative species of the stem group of *Ficus*, identifying multiple hybridization events throughout the evolutionary history of figs over 75 million years. Their co-phylogenetic reconciliation analyses revealed incongruent phylogenies between the host plant and the wasp, suggesting frequent host switching by obligate pollinators. The prevalent hybridization throughout the evolutionary history of *Ficus* mediated by host shifts of wasp pollinators provided new insights into our understanding of the co-divergence of interactive plants and pollinators. Given that *Ficus* is very diverse, a dominant tree species in tropical communities, additional studies of co-phylogenetic reconciliation involving more species would be helpful to understand the underlying mechanisms for coevolved mutualism.

(2) Sexual deception in orchid pollination

Orchidaceae is one of the most species-rich families with specialized pollination systems. For example, the coadaptation between long nectar spur orchids and long-tongued hawkmoth pollinators is a classic “arms-race” coevolutionary relationship (Figure 5C). In unusual sexually deceptive pollination systems, orchid flowers do not offer a food (nectar) reward but release floral odors that mimic insect sexual hormones to lure pollinators (Figure 5D). Early studies confirmed sexual deception in Australian and European orchids. For example, *Chiloglottis trapeziformis* flowers emit odors (2-ethyl-5-propylcyclohexan-1,3-dione) that mimic the female thynnine wasp *Neozeleboria cryptoides* to lure males for pseudo-copulation (Schiestl et al., 2003). Recent studies revealed chemicals emitted by plants in multiple pseudo-copulation systems on other continents. In South Africa, *Disa forticaria* is a rare orchid, pollinated by a male long-horn beetle (*Chorothyse hessei*, Cerambycidae). Male beetles are attracted by (16*S*,9*Z*)-16-ethyl hexadec-9-enolide, an odor chemical emitted by the orchid (Cohen et al., 2021). In Western Australia, the orchid *Pterostylis orbiculata* offers a very unusual tricosatriene to sexually deceive the male fungus gnat *Mycomya* species (Mycetophilidae). Four extra-long-chain hydrocarbons enhance the sexual behavior of gnats (Hayashi et al., 2021). In the Peruvian Andes, the orchid *Telipogon peruvianus* looks like a female tachinid fly on the daisy inflorescence (the food resource). Its volatile compound mimics the sexual hormone of tachinid flies (Martel et al., 2019). To date, genomic evidence for sexually deceptive pollination systems remains unidentified.

(3) Bird pollinators and flowers

The coevolution between birds and flowers is an evolutionary topic that has long been of interest to biologists

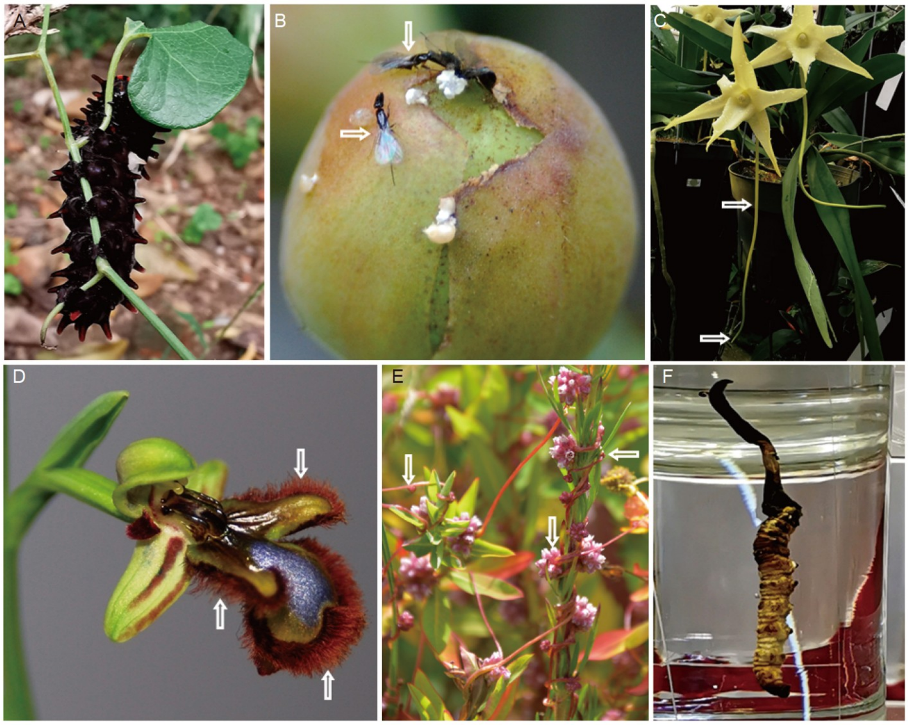

Figure 5 Model systems for coevolution studies. A, The coevolution concept originated from the study of plant–herbivorous insect interactions. Here, a butterfly larva of *Pachliopta aristolochiae* feeds on leaves of *Aristolochia debilis*, which contains toxic secondary metabolites deterring predators. B, Fig-fig wasp mutualism h0as been well-studied in recent years with comparative genomics. Here, three fig wasps (white arrows) are trying to enter an hypanthodium of *Ficus benjamina*. C, The reciprocal selection between the long-tongued pollinator and long-corolla-tube (marked with an arrow) has been hypothesized since Charles Darwin (1862). Here, the Darwin orchid (*Angraecum sesquipedale*) produces a nearly 30-cm nectar spur. D, In the flower of *Ophrys speculum*, an orchid evolving sexually deceptive pollination, the lower petal (labellum, arrows marked) resembles a solitary female bee in *Andrena* or in *Colletes*. It emits a floral odor with components similar to insect sexual hormones that can lure naïve pollinators to copulate. E, A flowering dodder (here *Cuscuta japonica*, arrows marked), typical of parasitic plants that are root- and leaf-less using functional genes from the host plant. For example, they flower synchronously, perhaps due to the transfer of host-synthesized FLOWERING LOCUS T protein into the dodder. F, A traditional Chinese medicine (Dongchong Xiacao) is a symbiont in which one fungal species (*Ophiocordyceps sinensis*, upper part) parasitizes the moth larvae of *Thitarodes* (Hepialidae) species. These six photos are credited to Shuang-Quan Huang.

(Krauss et al., 2017). A well-known example is bird pollinators' foraging preferences and the flowers' rewards. The main lineages of the nectar-sucking bird, hummingbird, sunbird, honey-eater, flower-piercer, and lorikeet are thought to be involved in coevolution (McWhorter et al., 2021). A comparison of 50 flying-bird species from the New World, Africa, and Australia showed that species with smaller intestine areas generally had a greater ability to dehydrate sucrose and higher sucrase activity per unit of intestinal area. Convergence analysis showed high sucrose hydrolysis and activity per unit of intestinal surface area in specialist nectarivores, matching the high proportion of sucrose in the nectar of the plants they pollinate. However, plants pollinated by generalist nectar-feeding birds in the Old and New Worlds secrete nectar mainly consisting of glucose and fructose. Matching the intestinal enzyme activity in birds with the nectar composition in flowers is an example of convergent coevolution between plants and pollinators on an intercontinental scale (McWhorter et al., 2021).

Another coevolutionary pattern between birds and plants is the shape and size of the bill and bird-pollinated flowers, which is especially well-studied in hummingbirds (Rico-Guevara et al., 2021). A Caribbean hummingbird (*Eulampis jugularis*) has one of the most sexually dimorphic bills. Temeles and Kress (2003) proposed the reciprocal selection of bill and floral tube morphology between *E. jugularis* and its pollinated *Heliconia* flowers. Male birds with short, straight bills are the sole pollinators of *Heliconia caribaea* with short-tube corollas, while flowers of *H. bihai* pollinated by female birds are large with long-tube corollas.

(4) Early angiosperms and pollinators

The interaction between early angiosperms and pollinators could shed light on flower evolution. To construct a cophylogenetic relationship with pollinators in Schisandraceae, the largest early-diverging angiosperm family, Luo et al. (2018) studied changes in plant-pollinator interactions across multiple sites and years. The interaction between gnats and Schisandraceae started in the early Miocene (23 Ma). Most species are pollinated by gnats that lay eggs on flowers, and their larvae feed on the secreted liquids of flowers. Usually, one plant species uses a unique gnat species as its pollinator, but some species shift to beetles (Luo et al., 2018). This co-divergence study suggested that pollinator shifts could drive species diversification even in early-diverging angiosperms.

(5) Mutualism between plants and fungi

Many plants form mutualistic mycorrhiza with fungi. Usually, the fungus utilizes organic material generated by photosynthesis from the plant. In some cases, however, plants are "mycoheterotrophic," exploiting the fungal partner with carbon flow from the fungus to the plant. Suetsugu and Matsubayashi (2021) used molecular barcoding of C^{13} and N^{15} to physiologically and ecologically investigate a photosynthetic orchid, *Apostasia nipponica*. They found that Apostasioideae plants retrieve carbon from both photosynthesis and the fungus at the adult stage. Both holomycoheterotrophic *Cremastra aphylla* and photosynthetic *C. appendiculata* extracted carbon from fungi via dead wood (Suetsugu et al., 2022). The relationship between fungi and plants is ambiguous; typically, the fungus is saprophytic, and the plant is photosynthetic. However, the direction of carbon flow between the plant and its partner fungus can be intriguing. If carbon flows from the fungus to the plant, the traditional mutualism between plant and fungus should be reconsidered and may be "predation". Additional studies should investigate whether the reverse carbon flow of fungi to plants commonly appears in plant-fungus interactions.

(6) Mutualism between plants and symbiotic bacteria

Nitrogen is one of the major limiting nutrients in plant growth (Leghari et al., 2016). The biological process responsible for transforming molecular nitrogen into ammonia is referred to as nitrogen fixation. Nitrogen-fixing bacterial species are diverse and widespread and colonize the rhizosphere and interact with plants. Fabaceae and actinorhizal plants can obtain nitrogen through their association with rhizobia or *Frankia* to modify a specialized organ, i.e., the root nodule of host plants. Other symbiotic associations involve heterocystous cyanobacteria. The root surface contains large numbers of nitrogen-fixing species, but the root interior of a variety of cereal crops and pasture grasses has also been observed to contain these species (Franche et al., 2009). To understand the adaptation of nitrogen-fixing bacteria to legumes, the host may select a microbiome with more cooperative features. In one study, the nitrogen-fixing bacteria *Ensifer melioti* was paired with five genotypes of *Medicago truncatula* to test differences in the selective strength of these genotypes in cross-infection experiments (Batstone et al., 2020). Independent of host selection (the different selection strength of host genotypes to the parasite), the nitrogen-fixing bacteria *Ensifer meliloti* quickly adapted its local host genotype and later, its microbiome became more beneficial to the host (if it shares an evolutionary history with its host). This study implied that cooperation depends on the partner's genotype and could be strengthened by the local adaptation of nitrogen-fixing bacteria to local hosts (Batstone et al., 2020). Mutualistic root association with nitrogen-fixing bacteria is a highly desirable trait to be introduced into major (cereal) crops. A better understanding of plant and nitrogen-fixing bacteria interactions in a coevolutionary framework would increase crop yields via more efficient nitrogen fixation.

Predation

The concept of "coevolution" was first coined for predation (Ehrlich and Raven, 1964) in a report describing Brassicaceae species and butterfly larvae in which a detoxication mechanism evolved in herbivores to mediate adaptive radiation in plants. However, this remains experimentally unconfirmed. If herbivore-driven changes in host plant secondary chemistry form a new plant lineage, two main classes of mechanisms, pre- and postzygotic, may be involved. The prezygotic mechanism applies mainly to the sympatric speciation model, while postzygotic applies to a parapatric or allopatric model. Studies of *Dalechampia* and its herbivores and pollinators (Armbruster, 1997) and the patterns of specialized defense of tree species in the Peruvian Amazon to herbivores in different habitats (Fine et al., 2004) provide evidence for the original hypothesis of Ehrlich and Raven (1964). Interestingly, these mechanisms are more likely at low latitudes and are thus more likely to produce new species in the tropics. A predictive framework for further studies has been outlined for the general role of herbivores in the diversification of host plants (Maron et al., 2019; Marquis et al., 2016).

To survive and reproduce, flowering plants must balance escaping herbivores and attracting pollinators. Due to the effect of herbivore damage on vegetative growth, reducing resource allocation to flowers or increasing investment in chemical defense is favored. If plant defenses hurt pollinators and repel foraging behaviors, increased investment in pollinator attraction is favored under a scarcity of pollinators. In other words, herbivores affect the phenotype of flowers, which affects pollinators. Pollinator health, life history, and coevolutionary history result in context-dependent chemical environments for plant defense (Jacobsen and Raguso, 2018).

Like Erhlich and Raven's study of coevolution between plants and herbivores, the monarch butterfly and its host plant milkweed (*Asclepias*) have evolved in an "arms-race" relationship for chemical defense and detoxification. The toxin in milkweed affects the growth and egg-laying of the butterfly *Danaus plexippus*. Agrawal et al. (2012) found that 40% of leaf cardenolides in *Asclepias curassavica* are voruscharin, while monarch caterpillars could convert voruscharin into calotropin and calactin. The toxin from milkweeds was not detrimental to the caterpillar but restricted their growth. The monarch has >50-fold enhanced resistance to cardenolides compared with sensitive animals that are absent for voruscharin, suggesting a highly specific plant defense.

Collectively, our understanding of plant–herbivore interactions remain at the level of identifying the relevant chemicals, especially toxins and antidotes. Additional studies of coevolution in chemical interactions between herbivores and host plants will be fruitful with the development of finer-scale metabolomics.

Parasitism

(1) Horizontal gene transfer

Studies have shown that plant genomes have undergone HGT between species, especially in parasitic plants that have lost some genes but utilize functional genes of the host (Figure 5E). This may be facilitated by the intimate physical association between parasites and their hosts. 1) Plant mitochondrial genes. Plant mitochondrial genes are transmitted horizontally across mating barriers between species with surprising frequency caused by direct physical contact between the host and the parasite (Davis and Xi, 2015; Mower et al., 2004). 2) Nuclear genes. A phylogenomic study of *Rafflesia cantleyi* (Rafflesiaceae) and its relatives that are obligate parasites and possess the world's largest flowers showed that about 2.1% of the nuclear gene transcripts were likely acquired from its obligate host (Xi et al., 2013). 3) Transcriptomes. The parasitic plant *Cuscuta pentagona* (dodder) exchanges large proportions of its transcriptome with hosts, including *Arabidopsis thaliana* and tomato, in a potential mechanism for RNA-based interactions between species and HGT (Kim et al., 2014). 4) Proteins. Liu et al. (2020) found that from hundreds to >1,500 proteins were transferred between dodder and the host plants Arabidopsis and soybean, and hundreds of inter-plant mobile proteins were detected in the dodder seeds and the host soybean. Different hosts bridge-connected by dodder were also found to exchange hundreds of proteins. These results suggest that large-scale inter-plant protein translocation may play an important role in interactions between host plants and dodder and even among dodder bridge-connected hosts (Liu et al., 2020). Generally, plant-parasite interactions occur via HGT in parasitic plants, typically the dodder.

As another example, the valuable traditional Chinese medicinal herb *Ophiocordyceps sinensis* is a fungal species parasitizing the moth larvae of the genus *Thitarodes* (Figure 5F), mainly occurring in alpine meadows on the Qinghai-Tibet Plateau. Understanding the molecular mechanisms in this unique symbiosis would be helpful for artificial cultivation and *in situ* conservation, given that human over-exploitation has caused the rapid decline of wild populations in the last two decades.

(2) Regulated factors

Dodders (*Cuscuta*, Convolvulaceae) are root- and leaf-less obligate parasitic plants that sponge water and nutrients from the stems of host plants via specialized feeding structures called haustoria. The haustoria of dodders could facilitate the bidirectional movement of viruses, proteins, and mRNAs between hosts and parasites. One study showed that *Cuscuta campestris* haustoria accumulated high levels of novel microRNAs (miRNAs) while parasitizing *A. thaliana*. These miRNAs acted as trans-species regulators of host gene expression, suggesting that they may act as virulence factors during parasitism (Shahid et al., 2018). Dodders parasitize different host species with varying flowering times. Remarkably, one dodder species (*Cuscuta australis*) synchronizes flowering with that of its hosts. Shen et al. (2020) revealed that the flowering locus *T* functioned as an important interspecific flowering signal in host-dodder interactions. The unique flowering regulation of dodders illustrates that retrogressive evolution in parasites may facilitate the physiological synchronization of parasites and hosts, allowing *C. australis* to align its reproduction time with its host. However, whether synchronic co-flowering optimizes the fitness of parasites is unclear. Additional genetic regulation examples mediated by HGT will likely be revealed in the future.

(3) DNA fossils

Sapria himalayana Griff. (Rafflesiaceae) is an endosymbiont without a vegetative plant part. Its pattern of gene loss was recently observed as similar to that of other parasitic plants (Cai et al., 2021). Most of the *S. himalayana* genome is highly simplified, and the remaining genome contains very long introns. These horizontally transferred introns are informative to identify extinct hosts and can be used as "DNA fossils" to investigate extinct mutualists (Cai et al., 2021). Given that so many species have vanished in the evolutionary history of life, "DNA fossils" could help us discover species that interacted with parasitic plants but left no fossils in the ground.

(4) Insects using plant's spears to pierce through plant's shields

Plants are eaten by many insects and produce a series of toxic secondary metabolites to protect themselves from herbivory. Xia et al. (2021) found that a polyphagous agricultural pest could hijack a plant detoxification gene that neutralizes plant toxins (phenolic glucoside). The insect whitefly (*Bemisia tabaci*) is a vector for multiple serious plant viruses, recognized as the second most harmful pest by the Food and Agriculture Organization of the United Nations (FAO) and is a so-called "super pest" in agricultural ecosystems. A series of studies of molecular evolution, biochemistry, and metabolism revealed the host-adaptation of the whitefly to its hosts (Xia et al., 2021). The secondary metabolite phenolic glucoside is poisonous to the whitefly, but the whitefly uses the plant-sourced HGT *BtPMaT1* to detoxify phenolic glucosides. Too much phenolic glucoside is also detrimental to plant growth and development, so plants must metabolize phenolic glucoside. Once insects "learned" how to detoxify phenolic glucoside from plants, the defense of plants turns collapsed to insects. These results revealed an evolutionary prospect: herbivores use the genetic toolkit of their hosts to counter host defenses. From the perspective of coevolution, parasitic insects are apparently piercing the shield of plants using the plants' spear, tearing a huge leak in the interaction between insects and plants, and the balance has leaned severely to the insects. It's not hard to predict that hosts may handicap countermeasures for such a smart parasite, which remains to be explored in the future.

(5) Fungus parasitism in plants

The interaction between plants and fungi may be at the gene-to-gene level. Many pathogenic microbes have evolved genomes with highly variable regions enriched in TEs and pathogenicity-related genes. Similar transposable-element-rich regions that mediate accelerated evolution have been observed in plant genomes. In these regions, immune receptor genes typically reside. Various mechanisms have been identified by which TEs contribute to the coevolution between plants and their associated microbes (Seidl and Thomma, 2017).

Anther-smut fungi are a powerful system to study host-pathogen specialization and coevolution. Hundreds of *Microbotryum* species specialize in diverse plant species in Caryophyllaceae, castrating their hosts by manipulating the reproductive organs to facilitate disease transmission. A recent study using a combination of comparative genomics, population genomics, and transcriptomics approaches revealed the integration of different evolutionary perspectives across different timescales in anther-smut fungi and host plants (Hartmann et al., 2019).

(6) Virus parasitism in plants

Plants have evolved sophisticated surveillance and defense mechanisms against constant attacks by microbial pathogens, including viruses. Nucleotide-based RNA silencing and receptor-based innate immunity constitute primary plant defenses to viral infections (Ding, 2010). Plant viruses also have evolved virulence strategies to suppress host defenses to establish infections. This coevolutionary arms race between plant hosts and viruses has shaped the multifaceted defense and counter-defense mechanisms observed today (Cheng and Wang, 2017). Plants and viruses coevolve, given that selection favors plant defenses against the deleterious effect of viruses on plants. Most evidence for plant-virus coevolution derives from highly virulent viruses in agricultural systems, in which genetically modified crops influence or mediate genetic changes in the virus population. Studies have focused on virus responses to qualitative resistance (either dominant or recessive); however, within this restricted scenario, analyses of the population genetics of pathogenicity and resistance factors remain scarce (Fraile and García-Arenal, 2010). One core question between plants and viruses is under which circumstances do viruses generate selection by wild plants. It is challenging to study whether qualitative resistance is a major defense strategy against virus infection in nature or if characterized genes determining qualitative resistance to viruses evolve in response to virus infection (Fraile and García-Arenal, 2010).

Plants and viruses could be mutualistic in wild ecological systems, while viruses are usually pathogens in agricultural systems. A recent study showed that plant viruses could also be pathogens under natural conditions. One study focused on wild *Arabidopsis* and cucumber mosaic virus (CMV) and investigated the resistance and tolerance of *Arabidopsis* genetic diversity to CMV. They found that the resistance and tolerance of *Arabidopsis* to CMV varied among populations and was determined by the interaction between virus and host genotypes (Montes et al., 2019). Resistance and tolerance with co-occurring independent features have evolved independently from related life history traits that were adaptive to climatic changes. Given that the virulence of some viruses in the wild has been determined, the pathology of plant viruses in a coevolutionary framework will be studied more in the future.

Theoretical and methodological advances in coevolution

Theoretical advances in coevolution largely depend on studies of model organism-related coevolution, especially bacteria-virus coevolution systems. These studies have explored the relationship between coevolution, molecular evolution, and genomic evolution (e.g., Laanto et al., 2017; Paterson et al., 2010). For instance, using a bacteriophage system, Paterson et al. (2010) found that the molecular evolution rate in the phage was much higher when the bacterium and phage coevolved, and the most rapidly evolving phage genes under coevolution were involved in host infection. Studies have long lacked quantitative measures of the strength and prevalence of coevolution. Week and Nuismer (2019) developed a novel method that derives maximum likelihood estimates for the strength of direct pairwise coevolution by coupling a coevolutionary model to spatially structured phenotypic data. They tested this method using two interactive systems of mutualism and predation.

Theoretical studies of mutualism and parasitism have been explored more than those of predation and competition. Guimarães et al. (2011) modeled coevolution in mutualistic networks and found that coevolution shaped species traits and resulted in higher trait complementarity and trait convergence of species in the same trophic level, and convergence was higher in the presence of super-generalists. Furthermore, Medeiros et al. (2018) studied how gene flow and geographical variation in selection affected trait patterns in mutualistic networks and found that gene flow favored trait matching, especially among generalist species in species-rich networks such as pollination and seed dispersal interactions. They also found that the gradual loss of gene flow was associated with habitat fragmentation and may hurt coadaptation in mutualisms. Morran et al. (2011) used experimental coevolution to test the Red Queen hypothesis. They found that coevolution with a pathogen rapidly drove obligately-selfing populations to extinction, whereas outcrossing populations persisted through reciprocal coevolution.

Trends and prospects

Roles of noncoding DNA/RNA, SVs, and epigenetic modifications

The past ten years have witnessed rapidly increasing studies on the molecular mechanisms of adaptive evolution in wild animals and plants. These studies have provided in-depth insights into specific molecular evolutionary mechanisms of representative adaptive traits and the principles of molecular evolution, such as the repeatability and predictability of molecular evolution. Generally, most molecular mechanisms of adaptive evolution have been examined at the protein-coding gene level, including but not limited to amino acid substitutions, positive selection, rapid evolution, pseudogenization, gene loss, and differential gene expression. However, noncoding regions such as regulatory regions also play important roles in the evolution of adaptive traits through the evolutionary analysis of CNEEs (e.g., Sackton et al., 2019). SV may be a key driver of adaptive traits based on long-read sequencing techniques (e.g., Funk et al., 2021; Todesco et al., 2020). Noncoding RNAs and epigenetic modifications are also related to variation in important traits (e.g., Naish et al., 2021; Yu et al., 2020). Thus, molecular mechanisms will be observed and described more frequently with the rapid assembly of chromosome-level high-quality reference genomes and the development of analysis methods.

Integration of evolution, genetics, and development

Comparative genomics and population genomics analyses have identified many candidate genes potentially responsible for the adaptive evolution of species or the local adaptation of populations. However, to uncover the molecular mechanisms controlling adaptive traits, only identifying potentially important candidate genes is insufficient because some candidate genes might be false positives or one candidate gene is only a part of a multiple-gene complex mechanism and plays a minor effect. In context, the study of evolutionary developmental biology (Evo-Devo) is re-blossoming (Wei et al., 2020) and aims to uncover the genetic and developmental mechanisms of important traits from the perspective of evolution. These interdisciplinary studies focus on developmental mechanisms and phenotype reproduction rather than only on candidate genes. Currently, relatively few evolutionary studies have revealed developmental mechanisms or reproduced the mutant phenotypes in cell lines or animal/plant models (e.g., Kvon et al., 2016; Nakamura et al., 2016). This field is trending from performing "omics-based bioinformatics studies" to conducting Evo-Devo studies to uncover the molecular and developmental mechanisms of adaptive traits. Functional validation of candidate genes identified by "omics studies" should be done using biochemistry, cell biology, genetics, or mutated animal/plant models. The expected outcome is candidate-involved functional pathways or reproducing the studied trait in models, thus confirming the key role of these candidate genes or excluding false positives. Furthermore, the evolution of confirmed candidate genes or molecular mechanisms may mirror the evolution of adaptive traits across different taxa on different evolutionary time scales. Additionally, accurately measuring the phenotype of some adaptive traits or adaptations is difficult. Multidisciplinary studies are needed to elaborate on the processes and outcomes of adaptive evolution.

Mechanistic insights into coevolution between host and gut microbiota

With the development of next-generation sequencing technologies, the structure and function of gut microbiota can be revealed without large-scale experiments. Coevolution between hosts and gut microbiota is becoming one of the hottest research topics in evolutionary biology. One reason for this is that more and more studies have found that gut microbiota plays an essential role in host evolution and health. Currently, analyzing the structure and function of gut microbiota using *16S* rRNA gene sequencing and metagenomic sequencing is routine. The results help describe the patterns of structure and function and their correlation with host changes. However, the intrinsic mechanisms or functional pathways by which gut microbiota or hosts affect each other have remained largely unclear. The trend is to explore how hosts and gut microbiota interact or coevolve using experimental methods such as gut microbe *in vitro* culture or fecal microbe implantation in germ-free mice (e.g., Huang et al., 2022).

Meta-analysis and the proposal of new methods and evolutionary theories

With the emergence of an increasing number of species-targeted adaptive evolution studies in wild animals and plants, scientific communities expect general rules about the molecular mechanisms of adaptive evolution. For example, what are the common mechanisms of high elevation adaptation, aquatic adaptation, or cave adaptation? What are the rules of genetic convergence for different phenotype convergences? What are common mechanisms for mutualism, parasitism, predation, and competition coevolution? These critical scientific problems require meta-analyses or summaries of published specific cases and evidence. Meta-analyses could collect targeted problem-related cases and use standard scientific data integration methods to compare data and arrive at general conclusions or viewpoints, which is feasible considering the continually increasing data.

Additionally, analysis methods are in high demand. First, the increase in reference genomes has enabled large-scale structural variation and chromosome evolution studies. These studies require developing structural variation identification and comparison methods and chromosome evolution methods to cope with the challenges of three-dimensional genomics (3D-genomics) (Zhang and Li, 2020). The assembly of telomere-to-telomere (T2T) genomes will provide in-depth insights into the evolution of repetitive sequences, centromeres, and telomeres (Nurk et al., 2022). Second, improved algorithms for the identification of adaptive evolution, convergent evolution, and coevolution are urgently needed because of false positives (e.g., Fan et al., 2021). For example, the reliable identification of positive selection signals, the impacts of background convergence on the identification of true genetic convergence, and the actual link of genetic coevolution between two species are among the urgently needed analysis methods. Although experimental functional verification could reveal reliable or false positive candidate genes or interaction mechanisms, functional verification often takes so long that better bioinformatic methods are more attractive to researchers. Third, insights into the general rules of adaptive evolution and the development of new methods would facilitate the development of new or updated evolutionary theories, for instance, about evolutionary repeatability and predictability, major-effect genes or genome-wide effects, and molecular interactions in coevolution.

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

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