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Review article

Integration and modularity and their role in speciation and evolutionary diversification

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Abstract

The evolution of diverse life requires biological variation upon which selection can act. Modularity and integration structure patterns of biological variation at every scale of biological organization. Whereas the relationship between patterns of phenotypic modularity and integration and the evolution of morphological disparity is well established, their broader effect on taxonomic diversity and speciation is less clear. Here we review the evidence for how trait covariation patterns can influence the process of diversification. Integration between ecological traits and reproductive traits is an essential element in creating reproductive isolation during ecological speciation, both in sympatry and allopatry. Modularity patterns influence the potential to generate new phenotypes, shaping the potential for rapid morphological and ecological change in adaptive radiations. Speciation via sexual selection can involve a complex process of breaking up and re-assembling phenotypic modules that comprise intraspecific signals. Finally, we discuss open questions about the relationship between modularity, integration and diversification, including how modularity might influence extinction rates.

Sections

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Introduction

One of the most important processes that generates and maintains biodiversity is natural selection on phenotypic traits[1–3]. For natural selection to occur, traits must be variable and have some heritable component[1]. Thus, to understand the patterns and processes of evolution and diversification, it is essential to quantify how trait variation – the raw material for selection – is generated within and between populations. Biological systems are modular, such that the many traits that make up an organism can be divided into semi-independent units, where traits within a unit (module) share stronger covariation with each other than they do with traits in other modules[4] (Fig. 1). Modularity is closely related to the concept of integration, which describes the strength of covariation among traits or sets of traits[5,6].

Modularity and integration are ubiquitous features of complex life. These patterns of clustered trait covariation are present at multiple scales of biological organization ranging from development to macroevolution (Table 1). Modularity has emerged as an active area of study in the field of macroevolution as the role of modularization in patterns of trait evolution has become widely recognized[7–13]. As such, researchers now have a fine-scale understanding of how traits might become compartmentalized or partitioned across different scales of biological organization, and of the underlying drivers of modularity in organismal design. Today, scientists can detect the variation of phenotypic modules, as well as track and quantify their evolution across hundreds of millions of years.

Research interrogating the macroevolutionary consequences of modularity and integration supports a consensus that the modularity of the genotype–phenotype map structures the ability to generate phenotypic variation, and how that variation might or might not coincide with changes in selection through time[14–18]. However, this research has focused primarily on understanding how the structure of phenotypic, developmental and genetic covariances influence phenotypic disparity, not taxonomic diversity. By contrast, the influence of the modular organization of trait variation on the process of diversification (that is, the origin and persistence of species) is less well understood.

In this Review, we explore how modularity is manifested at different levels of biological organization, and present evidence for the relationship between modularity, integration and diversity. We demonstrate that modularity and integration can influence patterns of diversity in three main ways. First, speciation can be the result of barriers to gene flow that are a consequence of natural selection on phenotypic or ecological traits that are strongly integrated with reproductive traits. Second, the modular organization of traits can facilitate the origin of new species via natural selection by shaping differential evolvability of some traits compared with others, thus creating the potential for ecological speciation in sympatry or allopatry. Third, the origin of sexually selected traits and speciation via sexual selection requires a complex pattern of breaking and building trait correlations through time. Modularity that separates the traits that are associated with survival and those that are related to reproductive isolation can therefore facilitate speciation via sexual selection. Finally, we highlight the unanswered questions about the relationship between modularity, integration and diversity to help to guide future research efforts.

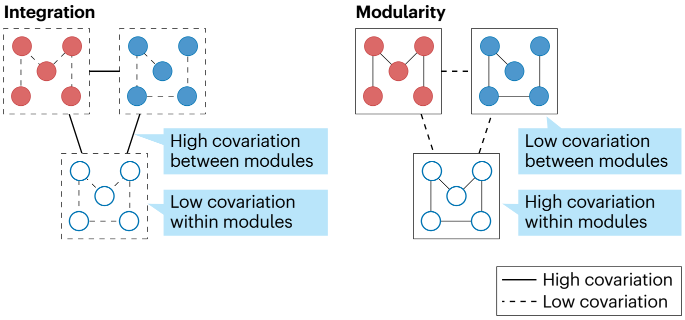

Fig. 1 | Integration and modularity among trait clusters. Integration occurs when there is stronger covariation or correlation between different trait clusters than within them, whereas modularity occurs when there is a stronger covariation or correlation within trait clusters than between them.

Types of modularity

Owing to its hierarchical nature, patterns of modularity can span several layers of biological organization. There are three major forms of modularity that either have a major role in species divergence or are a direct by-product of the lineage branching process. In this section, we introduce these forms of modularity, and compare and contrast these forms and their relationships to each other.

Developmental modularity

Developmental modules are sets of traits that share a common origin during embryonic growth. These modules can include structures that arise from a common embryonic cell population or those that share a response to morphogen gradients, or in other more experimental cases, regions of a developing embryo that can maintain their identities, cell fates and structures outside of their normal context (for example, in culture or in transplant)[14,19,20].

Developmental modules also help to modulate interactions between organismal phenotype and the environment. For example, developmental modules can funnel genetic and environmental perturbations along an integrated trait axis to produce a constrained range of characteristic phenotypic outcomes in *Drosophila* wings[21]. As such, these modules sit at a critically important interface between genetic variation and environmental perturbations and the resultant phenotypic outcomes. Developmental modules form the building blocks of an organism and are thought to represent the major targets of natural selection, and it is with these modules that organisms can adapt and change[22,23].

An important quality of developmental modules is that they are not static and instead can exhibit strong transient properties over the course of the development of an organism. This process, termed the palimpsest model, means that early patterns of modularity can be incompletely overwritten by newer patterns as embryos continue to grow and develop[24–26]. Such patterns have been observed in fish skull embryonic development, demonstrating that early patterns of developmental modularity are primarily defined by pleiotropic interactions before being largely overwritten by tissue–tissue processes associated cell migration and plastic responses to muscle forces[27–29]. Organisms are under constant selection throughout ontogeny, and the selective pressures acting at each developmental stage can vary. If the transient nature of developmental modularity imparts phenotypic plasticity or robustness to developmental perturbations, variation in developmental modularity could itself be adaptive[25].

Variational modularity

Variational modularity is in many ways the product of developmental modularity[27,30]. Variational modules are defined empirically as clusters of traits that exhibit stronger patterns of covariation within themselves

Table 1 | Definitions of various forms of integration and modularity and the hypothesized underlying processes that shape them

Term	Definition	Hypothesized drivers	Citations
Integration	Strong correlation, correspondence or covariation between traits	Functional coupling, pleiotropic interactions between traits, tissue–tissue processes	Olson & Miller[6], Klingenberg[129], Conith et al.[27–29]
Evolutionary integration	Co-evolution of traits between species or across generations	Functional coupling, pleiotropic interactions between traits, correlational selection	Olson & Miller[6], Klingenberg & Marugán-Lobón[5]
Developmental integration	Covariation between structures or traits in a developing embryo or across growth stages	Genotype–phenotype map, allometric scaling, tissue–tissue processes	Cheverud[130], Mitteroecker et al.[131], Hallgrímsson et al.[132], Conith et al.[27–29]
Variational modularity	Semi-independent parcellation of traits within a population	Genotype–phenotype map, linkage disequilibrium, functional independence, tissue–tissue processes, developmental plasticity	Olson & Miller[6], Wagner & Altenberg[37], Larouche et al.[31], Wagner & Zhang[38], Zelditch & Goswami[12]
Evolutionary modularity	Independent evolution of traits or trait clusters across generations or different species	Differential selective pressures, developmental constraints, functional independence, differential evolvability	Wagner & Altenberg[37], Felice & Goswami[39], Watanabe et al.[40], Evans et al.[71], Knapp et al.[45], Goswami et al.[46]
Developmental modularity	Semi-independent parcellation of traits or tissues within a developing embryo or across growth stages	Genotype–phenotype map, embryonic origin, tissue–tissue processes	Raff[19], Raff & Raff[14], West-Eberhard[20]

than they do with other traits[6,12]. Variational modularity is typically quantified among the reproductively mature adults within a population that exhibit terminal phenotypes that have been shaped by developmental and environmental processes throughout the life span of an organism[26,31]. Variational modularity therefore examines the average end points of developmental modularity across many individuals within a population[32], and it is at this level of biological organization that modularity theory has perhaps been the most developed. At the population level, variational modules are often a mix between result of pleiotropic interactions between gene networks that code for specific phenotypes and the environmental context and tissue–tissue interactions that ultimately produce these traits in a developing embryo[27,33,34]. Variational modules then can represent a mosaic of genetic and functional interactions between traits within a population.

Over successive generations, these variational modules are exposed to natural selection, which can allow for different trait clusters to respond to selection independently[4,35–38]. Systems that exhibit strong patterns of modularity are therefore considered to be more evolvable or elicit stronger responses to natural selection than those that are more integrated and less modular[12]. These variational modules are expected to be of particular importance during cladogenesis because they represent the building blocks that can be modified as species diverge, and the differences in evolvability between these modules can determine which sets of traits are able to generate more variation and respond more strongly to natural selection.

Evolutionary modularity

Evolutionary modularity and variational modularity represent distinct but related processes[12,32], where variational modularity occurs within a population, and evolutionary modularity occurs between species across macroevolutionary timescales[32]. Evolutionary modularity, therefore, represents the sum of variational modularity patterns across many populations or species. Alternatively, evolutionary modularity can describe traits that co-evolve, for example, because of underlying genetic correlations or co-selection[12]. Evolutionary modularity can tie into patterns of developmental or variational modularity when either of these patterns are conserved across deep macroevolutionary timescales[39,40]. Drawing a direct link between population level and macroevolutionary processes can be tempting. However, one should note that other factors such as extinction and anagenesis can weaken the relationship between variational and evolutionary modularity by the removal of intermediate phenotypes between extant species, or divergence away from ancestral phenotypes within a lineage[41–44]. Despite this weakness, evolutionary modules seem to be largely conserved across clades[8,40], and studies of evolutionary modularity have advanced researchers' understanding of how traits might evolve over deep time and the relative contribution of developmental or functional processes that could influence these patterns of trait covariation[39,45–47].

The genotype–phenotype map and speciation

The modular organization of the genotype–phenotype map can facilitate the origin of species via ecological selection. Consider a hypothetical example of two allopatric populations of a single species experiencing differential ecological conditions and thus selective pressures (Fig. 2). Genetic drift or natural selection acts on a phenotypic trait, driving the fixation of different character states in each population. When there is secondary contact between these populations, no intrinsic reproductive barriers will have evolved if this trait is a variational module with little covariation with other traits (Fig. 2a). In the absence of assortative mating[48], it is likely that these populations will hybridize and continue as a single species. By contrast, if the focal trait is strongly integrated with other traits related to reproduction, such as the timing of reproductive life history stages, the structure and function of genitals and/or gametes, or mate preferences, then barriers to gene flow can occur[49] (Fig. 2b).

Phenotypic traits that are under divergent selection that also contribute to reproductive isolation have come to be called magic traits and are thought to be under the control of magic genes[50]. Pleiotropy is believed to be a key factor in driving sympatric speciation via magic genes, and modelling analyses indicate that sympatric speciation can occur more frequently in the presence of pleiotropic interactions[51]. Magic genes have been reported across a wide range of species including butterflies, birds, snails, fishes and flowers[51].

One well-documented example of variational integration between a phenotypic trait and a reproductive trait leading to incipient speciation is the apple maggot (*Rhagoletis pomonella*). Ancestral populations of this species infest hawthorn fruits, whereas derived populations

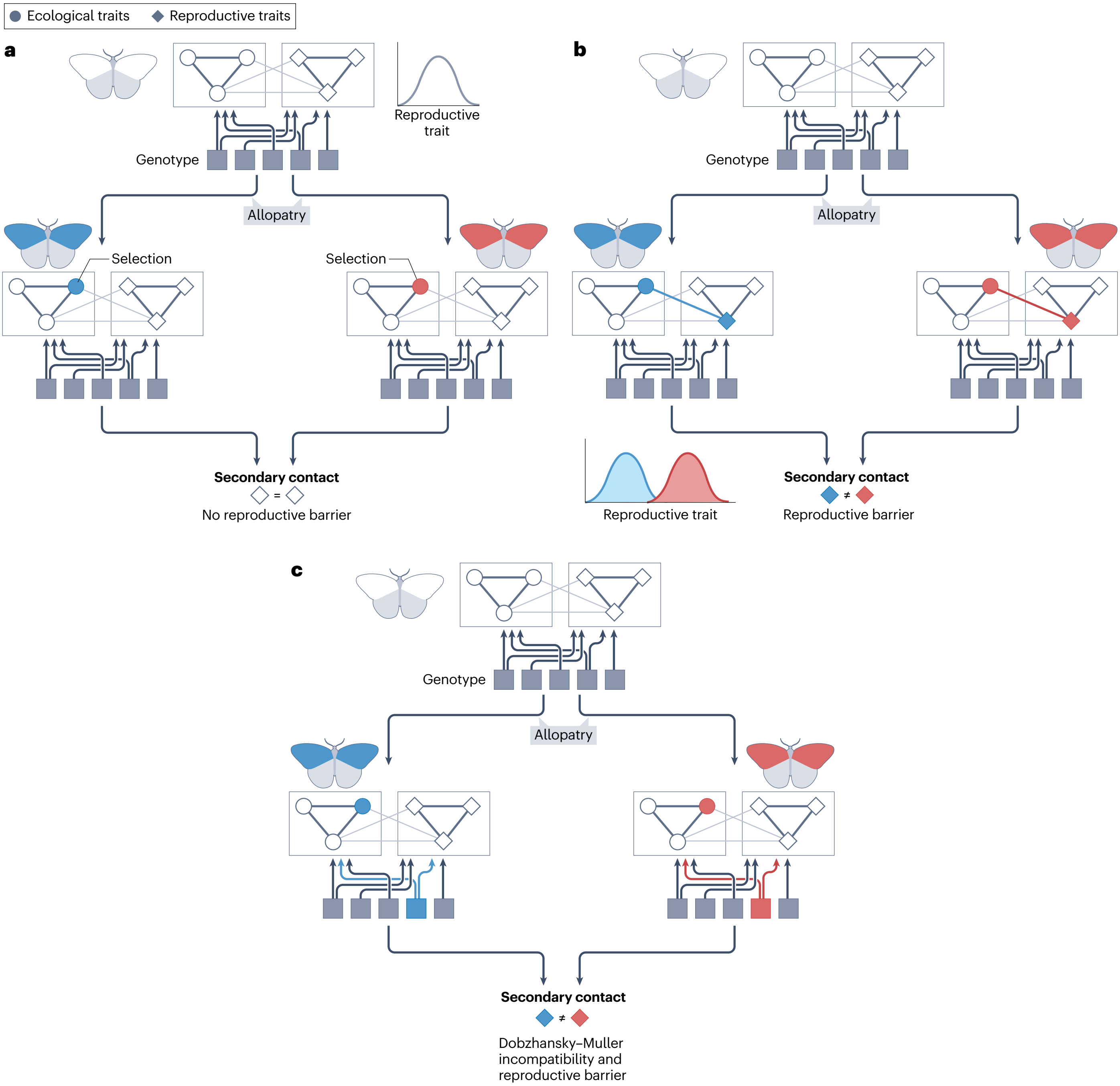

Fig. 2 | The modularity of the genotype–phenotype map can contribute to reproductive isolation. a, Considering ecological and reproductive traits as independent modules, divergent selection on an ecological trait in allopatric subpopulations (such as wing colour) will not result in reproductive barriers upon secondary contact. **b**, However, if ecological and reproductive traits are integrated, selection on ecological traits will cause a correlated response in reproductive traits, resulting in barriers to reproduction and gene flow and, potentially, speciation. **c**, Alternatively, selection on ecological traits can result in post-zygotic reproductive barriers via genetic incompatibilities.

attack apple fruits. Apples fruit a few weeks earlier in the spring than hawthorns, meaning that using this host requires *Rhagoletis* to evolve changes in phenology. Owing to genetic correlations between the intensity and duration of diapause, the apple and hawthorn populations can co-occur spatially but do not interbreed because they are active at different times of the year[52].

Stickleback (*Gasterosteus aculeatus*) populations in Western Canada represent another example of ecological selective pressures resulting in reproductive barriers due to variational integration between traits. Stickleback populations are distributed across several lakes that are ecologically similar in many ways, with the exception that some lakes host a sculpin species (*Cottus asper*) that directly competes with sticklebacks for resources[53]. Stickleback populations that live in sympatry with the sculpins are morphologically distinct from the populations that lack the sculpin, which have evolved to be more pelagic, probably because of competitive displacement[53]. In addition, when these distinct stickleback populations were reintroduced with each other experimentally, they exhibited strong assortative mating, preferring individuals from similar populations (with or without sculpins). Interestingly, the only aspect of body shape that predicts assortative mating frequency is the same aspect of variation that differs between the sculpin-sympatric and sculpin-free stickleback populations (shallow versus deep-bodied individuals). By contrast, aspects of body shape variation that are uncorrelated with the presence of sculpins have no effect on frequency of assortative mating. The integration between mate choice behaviour and one modular aspect of phenotypic variation seems to have kickstarted speciation in these stickleback populations[53].

Other examples include selection on flower colour causing a correlated change in flowering time[49,54] or correlated evolution of the brain and gonads[55]. Alternatively, divergent natural selection on ecological traits could result in reproductive isolation through hybrid incompatibility (Fig. 2c). First, differences between lineages or populations arise first through phenotypic divergence, which is only later accommodated by genetic differentiation[56]. The potential for phenotypic plasticity in the absence of genetic differences is possible only through variational modularity, in which the subunits that compose traits are recombined and remixed using existing developmental pathways without the need for mutations or genetic novelties[20]. Only later does the genotype accommodate the evolutionary response to selection[56]. A post-zygotic reproductive barrier forms if these new genetic variants are incompatible as hybrids[57,58].

Variational modularity and integration can influence the evolution of barriers to gene flow in sympatry in the same way. For example, in the warning coloration of two sympatric *Heliconius* butterfly species, genes associated with red warning coloration are located close to genes associated with mate choice and are pleiotropically linked[59,60]. Coupled with the strong colour-based assortative mating exhibited in these butterfly species, the linkage of these genes can create pre-zygotic barriers to gene flow[61,62]. Hybrids are actively selected against by parental species who show strong mating preferences for similarly coloured conspecifics, and by predators because the hybrid colour patterns no longer resemble the warning coloration of the parental species. Together, these selections form a post-zygotic barrier to gene flow thereby maintaining reproductive isolation in sympatry[59].

The importance of the modularity of the genotype–phenotype map extends beyond the origination of reproductive isolation. Indeed, much of the modern understanding of how trait evolution is shaped by phenotypic trait correlations is inspired by and derived from theoretical and empirical work on related concepts from quantitative genetics. For example, the conditional evolvability, autonomy and coevolutionary dynamics of multivariate traits can be estimated by examining the phenotypic variance–covariance matrix (P-matrix), which is shaped by the underlying genetic variance–covariance matrix (G-matrix)[2,15,63]. Thus, all of the links between diversification, modularity and integration – correlated evolution of phenotypic and reproductive traits, the potential to generate new phenotypes alongside speciation events, and the origin and maintenance of sexual signals – can also be interrogated by directly examining the G-matrix and P-matrix and quantifying evolvability and autonomy of traits through a quantitative genetics perspective.

However, there are potential advantages of addressing these questions primarily from a comparative morphology lens. For example, some phenotypic correlation patterns do not map to the underlying the G-matrix[27], partially because of overprinting from the developmental and structural interactions that also shape phenotypic expression[27]. For this reason, investigating how modularity and integration influence diversification can benefit from phenotypically orientated investigations. Furthermore, focusing on trait correlations rather than quantitative genetics allows for the inclusion of extinct organisms[64,65]. Ultimately, investigations of diversification–integration links with modularity will benefit by modelling not only trait correlations but also performance and fitness gradients and their effects of speciation and extinction patterns[66].

Adaptive radiations

Adaptive radiations are special case of sympatric speciation in which a period of exceptionally fast cladogenesis is coupled with an increase in ecological and phenotypic variation[67–69]. As the modular organization of traits can have a critical role in how phenotypic variation evolves, there are many examples of modularity being implicated as an important factor in shaping adaptive radiations[11,70,71]. However, the specific role that modularity has within an adaptive radiation can vary depending on the clade and the specific context.

In some cases, these modules can function as building blocks that can be independently modified or specialized for particular ecological resources. For example, in San Salvador pupfishes (*Cyprinodon*), a generalist species gave rise to at least two specialist species that exhibit highly divergent diets, with one species that specializes on snail feeding and another that exhibits lepidophagy (feeding on the scales of other fish)[69,72,73]. Within this radiation, the oral jaws are under strong selection and exhibit rapid rates of evolution[72]. Despite these profound and rapid changes in form and function, patterns of variational modularity within the skull are highly conserved across the different species including hybrids[11]. In each of these species, the oral jaws clustered to form a single cohesive module that was weakly integrated with the other modules of the skull. The relatively independent variance of the oral jaws with respect to other parts of the cranial skeleton probably allowed the oral jaws to functionally specialize without negatively affecting neighbouring modules during their ecological diversification.

Although patterns of modularity are highly conserved among closely related species, patterns of evolutionary integration seem to vary more broadly across species at the macroevolutionary scale. Flatfishes, for example, adaptively radiated along with the other carangarian fishes after the end-Cretaceous mass extinction event 66 million years ago. Flatfishes evolved a significantly more integrated braincase than their non-flatfish relatives, probably owing to the evolution of their characteristic asymmetrical skulls[71]. The evolution of their skulls involved modifying multiple structures within the neurocranium simultaneously, all while maintaining a modular configuration that was conserved across all carangarians[71].

In contrast to pupfishes and flatfishes, which seem to have leveraged an ancestral modularity pattern to facilitate phenotypic evolution as part of an adaptive radiation, other adaptively radiating clades are thought to have instead evolved new modularity patterns. Icefishes[70], for example, exhibit more evolutionary modularity in the skull and jaw than other percomorph fishes. In particular, the premaxilla and maxillary bones that are particularly important for suction feeding are more weakly correlated with the other skull modules in icefishes than in their percomorph relatives. This shift in modularity occurred during the early Miocene (23 million years ago), a period of rapid glaciation in Antarctica[74]. This glaciation is thought to have driven the extinction of many marine vertebrate species that could not withstand the freezing temperatures[75]. Icefishes, however, were able to persist owing to the presence of antifreeze proteins in their tissues[76]. The icefish ancestors in the Antarctic were then exposed to an environment with fewer predators and fewer competitive species, which might have released them from earlier evolutionary constraints and allowed them to adaptively radiate. This radiation allowed icefishes to explore new dietary and habitat niches and rapidly adapt their skull shapes to exploit this new-found ecological opportunity, resulting in mosaic patterns of evolution where the maxilla and braincase exhibited rapid rates of evolution relative to the other bones in the skull[70].

Sexual selection

Some of the most important parts of the speciation process are reproductive isolation and barriers to gene flow[77] (even if reproductive isolation is not strictly necessary for speciation[78]). In many diversification events, reproductive isolation arises through sexual selection pathways[79–82] (Fig. 3), such as divergent sexual selection on signalling traits. Sexual signals can include elaborate morphological traits (horns, antlers, elongated tails and extended eyestalks), colour patterns and behavioural traits such as songs[83]. The origin and evolutionary trajectory of such signals are deeply linked with variational integration and modularity.

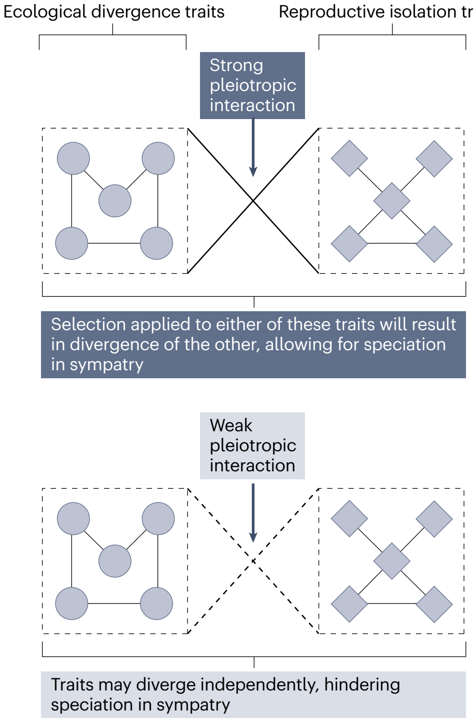

Fig. 3 | Modularity during sympatric speciation. Modularity can influence sympatric speciation by linking traits associated with eco-morphological function with traits associated with reproductive isolation.

First, signals can be variably developmentally integrated or modular with respect to the rest of the organism[84,85]. For example, ungulate horns and antlers are much more variable than the bones of the neurocranium upon which they grow[85]. Similarly, there is often weak genetic correlation between sexually dimorphic and monomorphic traits[86]. As these types of ornaments have high phenotypic variation, exhibit different allometric scaling patterns compared with non-ornamental structures, and respond to sexual selection when other traits do not, it seems intuitive that exaggerated ornamental structures are semi-independent modules[87]. However, ornamental structures (especially those that evolve via mate choice rather than intra-sex competition) also have an important role in signalling information about the quality of the individual to potential mates. Signals might contain information about the condition or health of the individual, the developmental mechanisms used to generate the ornament, or perhaps the genes of the individual[85,88,89]. For example, in animals, carotenoid pigments come from food, so females might initially prefer males with high-quality carotenoid-based colours because these signal good foraging capabilities of the individual mate[90]. Other condition-dependent signals might contain information about the ability to provide resources or territory[91]. To honestly convey this information about the individual, the ornamental trait and/or the developmental mechanism that generates it must be integrated with some other set of traits, genes or behaviours.

For sexually selected ornaments and signals to be both developmentally integrated with the overall condition and/or quality of the individual, and modular with respect to other somatic traits to be highly variable, there must be trait covariance. One hypothesis for the origin of this covariance is that signalling traits begin as condition-dependent integrated structures, become semi-independent modules, and then become re-integrated with other phenotypic traits[85]. First, the traits that are potential targets of sexual selection are those that are conspicuous, highly variable and integrated with condition and health[85] (Fig. 4a). An expected consequence of directional selection on such a trait is that the mean phenotype will increase (becoming larger, brighter or louder). At the same time, any developmental mechanisms that constrain the trait's continued exaggeration will be diminished. Likewise, new developmental mechanisms should arise to decrease the cost of trait expression. Together, these mean that the trait should become less developmentally integrated with other traits (Fig. 4b). This stage in the origin of sexually selected ornaments is supported by evidence for higher fluctuating asymmetry (a measure of developmental stability) in ornamental structures[92,93]. At this point, signals could begin to incorporate many different components, including sensory, aesthetic and informational aspects, each influenced by a combination of internal (such as developmental) and external (such as environmental) mechanisms (Fig. 4c). These mechanisms are expected to become more integrated over time, allowing for further elaboration and the evolution of greater morphological variation[85,94]. This evolutionary trajectory illustrates the complex ways that modularity and integration can shape — and be shaped by — sexual selection.

Multimodal signalling traits further demonstrate the modular nature of signalling traits. For example, a single visual cue might contain both a colour and a pattern, or a signal might consist of both a visual component (morphological trait) and an auditory component (song or call). Whether or not the individual elements of a multimodal signal are integrated with one another can vary across species. For example, there is a well-documented trade-off between song complexity and feather colour in some bird lineages[95], suggesting strong evolutionary integration. In other lineages, the evolution of these same traits is uncorrelated[96,97], suggesting that the diversity of sexual signals is shaped by lability of the modular organization of these complex traits.

Like signalling structures, genital organs are similarly shaped by developmental modularity as well as sexual selection, and can contribute to the origin of reproductive isolation[98]. Genital organs are extremely diverse and sometimes show species-specific morphologies in clades that might be indistinguishable on the basis of other morphological traits[99,100]. The modularity and morphological diversity[84] of genital organs relate to their multifunctional nature: copulatory organs are not simply tools to deposit sperm but are also involved in stimulation, sperm offence (male–male competition for sperm precedence), sperm defence (removal of rival sperm), clasping and courtship[84]. Critically, individual subregions or anatomical components of a genital organ can contribute to each of these functions in different ways[101,102] and can exhibit modular variation and, presumably, response to selection. For example, in the taurus scarab (*Onthophagus taurus*), some of the genital sclerites represent a developmental module related to sperm transfer whereas another genital sclerite acts to mechanically anchor the male to the female[103]. Similar within-structure variational and functional modularity of the genitals has been shown in other insects as well, with different segments being responsible for sperm offence and sperm defence[99,101,104].

The developmentally modular structure and function of genitalia have an important role in the morphological evolution of species-specific genital morphologies. One hypothesis for how genital organ evolution can contribute to reproductive isolation is through correlated evolution of male and female genital phenotypes (that is, an absence of evolutionary modularity)[105]. Under this hypothesis, subpopulations with divergent genital morphology would be unable to copulate. Perhaps surprisingly, there is weak support for such a lock-and-key style mechanism as mismatched genitals do not seem to be a major barrier to copulation or even insemination between incipient species[56,106,107]. Moreover, this hypothesis seems to necessitate the extremely high correlation between the morphology of male and female genital morphology within a population. In actuality, these traits tend to exhibit variational modularity and vary semi-independently, with males exhibiting higher variability than females[84] (although mammals are an exception to this pattern[108]). Instead of the lock-and-key mechanism, genital variation and evolution is thought to contribute to speciation through cryptic female mate choice and sexually antagonistic co-evolution (male–female conflict)[84,105,109]. Although modularity research has not often considered between-sex and within-sex morphological variation patterns, the co-evolution of male and female genitals represents an understudied type of variational and evolutionary modularity[110].

Summary and future directions

The structure of biological variation is influenced by modularity and integration at every level. It is therefore no surprise that biodiversity is shaped by modularity and integration. Likewise, the variance and covariance of traits shift and change, breaking apart and coming together, as lineages arise and evolve. Integration provides a mechanism to link ecological and reproductive traits during ecological and sexual speciation. Modularity compartmentalizes organisms into clusters of semi-autonomous traits that can mount differential responses to selective pressures. Together, organisms can use both integration and modularity to link functionally relevant traits together while reducing deleterious pleiotropic interactions between traits with different functions. In this Review, we have described the roles that integration and modularity can have during species divergence and have shown how these patterns of trait covariation can link and compartmentalize disparate traits to create barriers to sexual reproduction or allow for rapid sexual selection on subsets of traits without incurring deleterious effects on other traits. We additionally illustrate the role that integration and modularity have in adaptive radiations and the downstream effects of these patterns in shaping mosaic evolution across traits at the macroevolutionary scale.

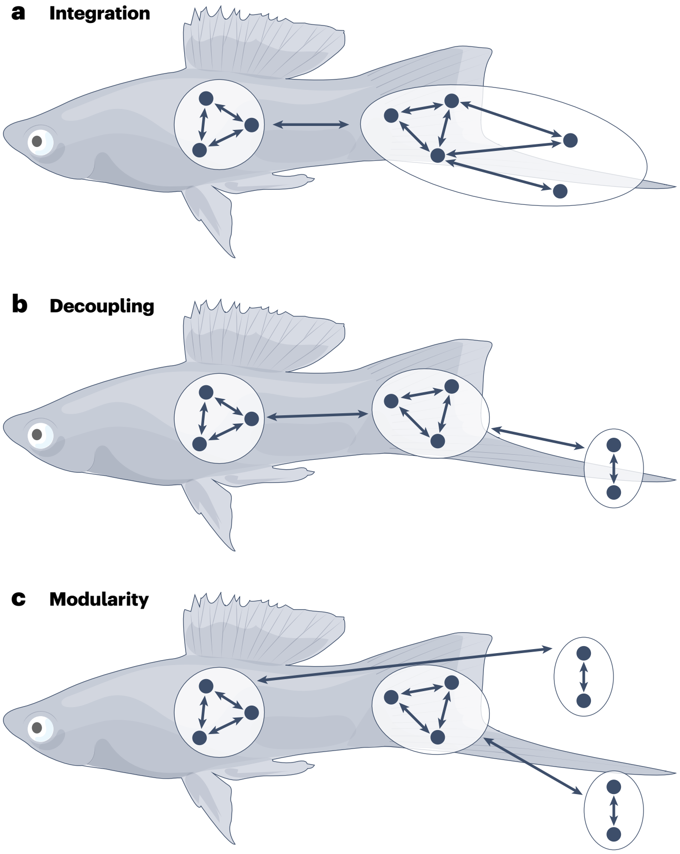

Fig. 4 | Modularity in exaggerated ornamental traits. a, Patterns of modularity in exaggerated ornamental traits are expected to change through time under the influence of sexual selection, illustrated here using swordtail fish. At first, mate choice will favour traits, such as tail length, that are tightly integrated with condition and fitness. **b**, Under sexual selection, the ornamental structure will become less integrated with the rest of the body as barriers to further elaboration and variation are selected against. **c**, Eventually, the individual aspects (traits) of the ornamental structure (such as colour, length or pattern) that convey different information will become separate modules, which are differentially integrated with developmental, genetic and metabolic aspects of the organism.

However, broader questions remain about developmental and variational modularity and their role in evolution. One of the prevailing questions centres around the evolvability of modularity patterns themselves, and the role of the environment in shaping patterns of modularity within a population. Whether modularity patterns themselves are indeed evolvable, and how these patterns might influence how evolvable and responsive a population might be, remain open questions. Advancing understanding here will enable researchers to better predict the circumstances that would promote the evolution of modularity.

Throughout this Review, we have focused on how modularity and integration influence the potential for speciation, but biodiversity depends on not only the origination of new species but also their persistence. How modularity and integration might relate to rates of extinction is still unknown. It is thought that high phenotypic plasticity might make species more robust to the threat of extinction in unpredictable environments[111]. Phenotypic integration can reduce phenotypic plasticity[112]. As such, it is possible that lineages with more modular phenotypes have lower extinction rates than those with less modular phenotypes, but this remains to be explicitly tested.

Likewise, the effect of trait correlations on speciation rates has yet to be explicitly modelled. Although there is an extensive literature modelling the relationship between trait values and diversification rates[113–116], it remains unclear whether the strength of integration and modularity among traits might bias diversification on macroevolutionary scales. Although the field of diversification modelling has been in upheaval over the past few years as the adequacy of methods has been probed in depth[117,118], there is some evidence that rates of speciation and modularity might be correlated. In cichlids, tooth complexity is not correlated with speciation rate but lability (that is, the ability to rapidly change between phenotypes) of tooth complexity[119,120]. Given that modularity and integration can influence phenotypic plasticity[112] and rates of phenotypic evolution[17,39,121], there could also be a link to speciation rates. Investigating this link will require further advances in multivariate trait-dependent diversification modelling[122].

Modularity and integration influence not only the process of diversification but also researchers' understanding and inferences about diversification processes. In phylogenetic systematics, estimation of divergence times has been improved by explicitly acknowledging the modular nature of the genome[123,124]. Relaxed clocks with character partitions allow different loci to evolve at different rates, generally improving the accuracy of phylogenetic analyses. For phylogeny reconstruction using morphological data, characters can similarly be partitioned[124–126]. Often, systematists partition traits based on regions of the body (for example cranial, axial and appendicular traits), implicitly assuming that the bauplan defines the boundaries between evolutionary modules. Some analyses are now using clustering methods to estimate the number of character partitions and their makeup[127]. More widespread adoption of this approach to morphological systematics alongside further methodological advances related to correlated trait evolution on trees[128] will further reveal how evolutionary modularity has shaped biodiversity.

We believe that further investigation into these areas and more will advance researchers' understanding of the role of integration and modularity during the lineage diversification process.

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The authors contributed equally to all aspects of the Review.

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