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Trends in Ecology & Evolution

Review

Conservation Evo-Devo: Preserving Biodiversity by Understanding Its Origins

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Unprecedented rates of species extinction increase the urgency for effective conservation biology management practices. Thus, any improvements in practice are vital and we suggest that conservation can be enhanced through recent advances in evolutionary biology, specifically advances put forward by evolutionary developmental biology (i.e., evo-devo). There are strong overlapping conceptual links between conservation and evo-devo whereby both fields focus on evolutionary potential. In particular, benefits to conservation can be derived from some of the main areas of evo-devo research, namely phenotypic plasticity, modularity and integration, and mechanistic investigations of the precise developmental and genetic processes that determine phenotypes. Using examples we outline how evo-devo can expand into conservation biology, an opportunity which holds great promise for advancing both fields.

The Timely Merging of Evo-Devo and Conservation Biology

Contemporary rates of species extinction are unprecedented and are predicted to continue to increase [1,2]. Such high extinction rates are largely attributable to anthropogenic disturbances, with conservation biology providing the theoretical and practical framework underpinning actions for the mitigation of biodiversity loss [3,4]. Conservation is an integrative field and has been notably enhanced by beginning to adopt evolutionary biology. This was especially the case during the 1990s when population genetics emerged and allowed the examination of gene flow within and among populations [5–7]. However, since this time evolutionary biology has itself been extended with the emergence of evolutionary developmental biology (i.e., evo-devo) mostly also during the 1990s. Evo-devo emerged to describe and understand how developmental processes bring about variation and change through evolution. Because evo-devo was still being established in the 1990s its interaction with conservation was not a priority nor likely possible.

With evo-devo now firmly established we contend that it can be used to understand how anthropogenic forces that impact on environmental variation ultimately impact on populations [8–12] (Figure 1). What currently seems to be underappreciated in the context of short temporal timescales is that shifts in environmental conditions should directly alter development both within and between generations by modifying how the phenotype relates to the genotype [i.e., the **genotype–phenotype (G–P) map**; see Glossary]. Such developmental changes should therefore significantly impact on the efficiency, rate, and direction of contemporary evolution [13]. Therefore, understanding what drives and underlies these developmental shifts could provide predictive insights into the evolutionary effects of anthropogenic disturbance. Such insights could indicate to managers which heritable variation should be targeted for protection

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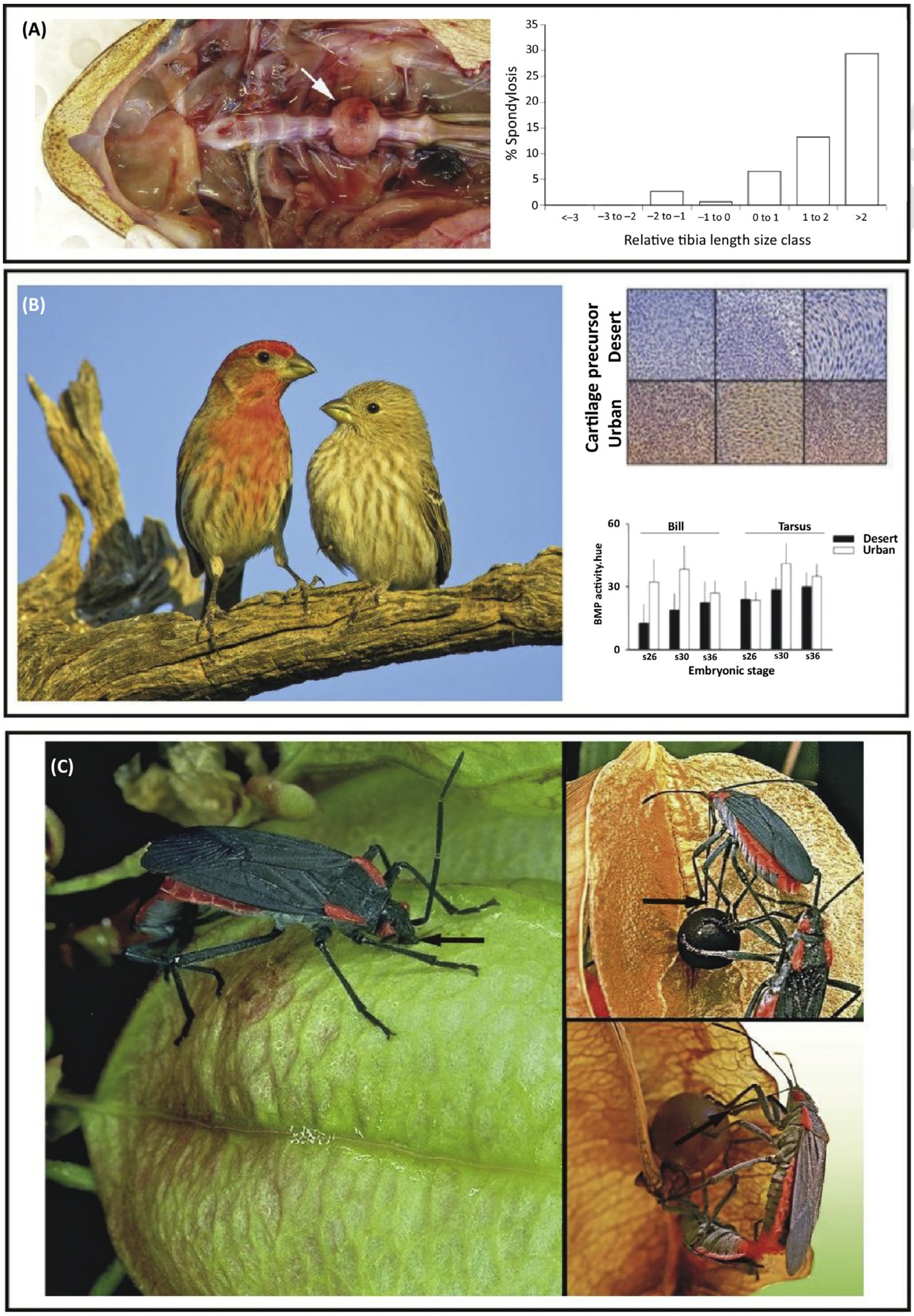


Trends in Ecology & Evolution

Figure 1. Anthropogenic Change Through the Lens of Evo-Devo. Environments induce evolution that can be measured through development. (A) Invasive cane toads (*Chaunus marinus*) develop spinal arthritis (left panel arrow) at far higher levels on the leading edge of the invasion where tibia length is significantly longer (right panel). This suggests an alteration of phenotypic integration between leg length and spines has a detrimental impact (photo courtesy of Greg Brown) [69]. (B) House finches (*Carpodacus mexicanus*) display divergence in bill morphology that corresponds to urban and desert habitats. The elevated levels of bone morphogenetic proteins (BMPs) during early bill morphogenesis, indicated by sections of bill primordia tissue with deeper staining in the upper right panel, are associated with the larger-beaked urban population. This is corroborated by quantitative measures of gene expression over development (lower right panel) [76] (photo courtesy of Alex Badyaev). (C) Soapberry bugs (*Jadera haematoloma*) show phenotypic change in their feeding

(Figure legend continued on the bottom of the next page.)

Glossary

Evolvability: the capacity of a population to produce adaptive variation through routes including mutation, standing genetic variation, and the input of environmental cues. Not to be confused with heritability, which is a measure of the total additive genetic variance. Q14

Functional genetics: a branch of genetics which investigates the properties and functions of genes and gene variations often in relation to phenotypes.

Genotype–phenotype (G–P) map: a metaphor for how the genotype relates to the phenotype. The G–P map is dynamic and can change depending upon the environment or ontogenetic stage of an organism.

Modularity: a module is a group of tightly correlated traits which are relatively independent from other such modules.

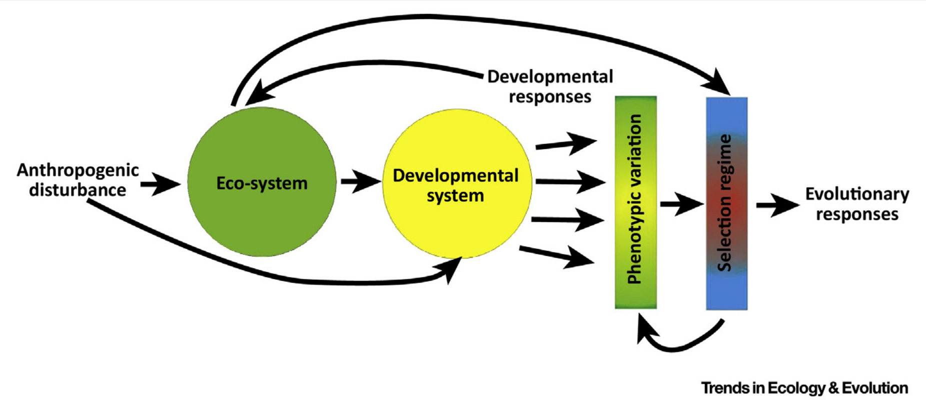
Niche construction: refers to how an organism can modify a community and in turn their own niche or the niche of other organisms.

Phenotypic integration: the correlation between phenotypic traits. This can be the result of developmental and functional interactions between traits that evolve.

Phenotypic plasticity: the ability of a single genotype to create multiple phenotypes through developmental responses to environmental cues.

Box 1. Evo-Devo Interactions with Environmental Change

Complex interactions between the environment and development can shape the phenotypic variation and, through subsequent selection, the evolution of a population. Anthropogenic disturbances can have direct effects on an ecosystem or a developmental system. However, there are also indirect effects whereby developmental responses can feed back onto the ecosystem and, in turn, affect the development of an organism through the reciprocal causation of niche construction. The ecosystem itself also affects the selection regime which acts upon the phenotypic variation produced by development to ultimately produce an evolutionary response (Figure I).



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through a precise understanding of developmental mechanisms and ecological conditions that impact on the G–P map and the fitness of populations [4,13,14] (Box 1). Further, the focus of evo-devo on understanding how sources of variation arise has much to offer conservation which focuses on preserving variation (i.e., biodiversity). This is because evo-devo has recently become more applicable to population-level approaches through its maturing theoretical focus and increased ability to account for continuous and complex phenotypic variation [15–17]. Evo-devo and conservation have the potential to form an important synergy, but what barriers to this might remain? We begin by briefly expanding upon the reasons why evo-devo and conservation have rarely interacted. We then highlight surprising conceptual overlaps between these fields and shift toward how three main areas of empirical interest in evo-devo (plasticity, **modularity** and integration, molecular mechanisms) can apply to conservation. Finally, we describe a way forward for evo-devo and conservation to productively work together.

‘Developmental Thinking’ Should Benefit Conservation

Developmental processes are undoubtedly affected by anthropogenic disturbances to environmental conditions, and would likely precede any demographic or evolutionary change (common monitoring tools in conservation) [12,13]. Thus, developmental change can serve as an ‘early warning’ signal for conservation [18]. However, connections between evo-devo and contemporary environmental change have rarely been made. As mentioned, this is probably for historical reasons, with evo-devo only beginning to permeate into mainstream evolutionary biology, let alone conservation biology. Indeed, reflecting this Fazey *et al*. [19] evaluated publication trends in conservation science and revealed that most research focused on species and populations, rather than on the broader suite of scales from molecules to ecosystems (but see Table 1). Thus, conservation science does not currently provide an understanding of how environmental stress impacts on organisms at a mechanistic level

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apparatus (arrows) as an adaptive response to utilize the invasive species of Taiwanese ‘flametree’ (*Koelreuteria elegans)* as a novel host (left-hand panel) rather than their native host (*Cardiospermum corundum)* (right-hand panels). Investigation of quantitative trait loci demonstrates that a relatively simple genetic change may underlie this evolution, with further developmental genetic studies yet to be conducted [80] (photos courtesy of Scott Carroll). Q15

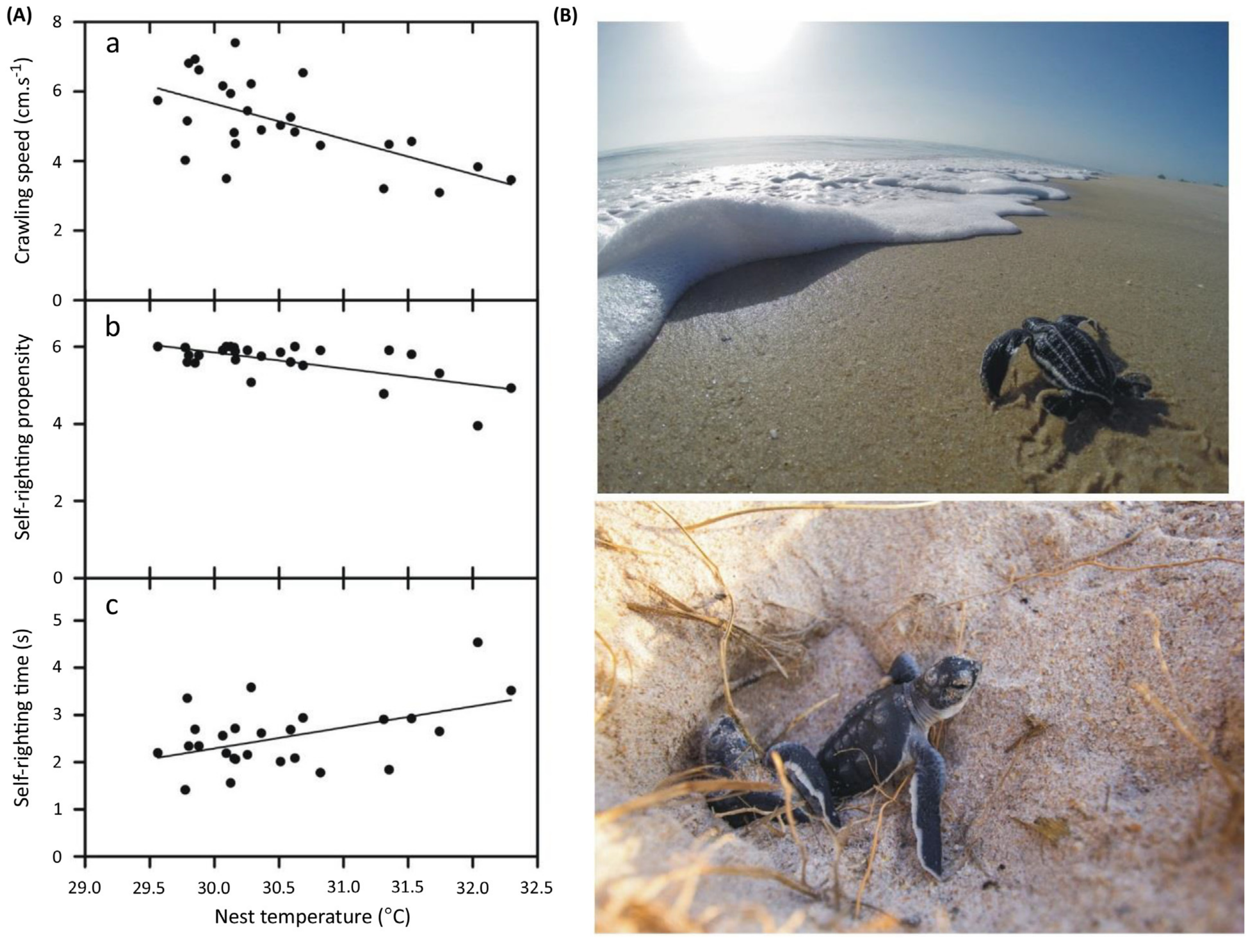
Q16 Table 1. Studies Reporting Developmental Changes Due to Anthropogenic Threats to Biodiversity[a]

Anthropogenic disturbance	Species	Trait	Mechanism	Evolutionary response	Adaptive?	Summary	Refs
Climate change	Reef fish *Neopomacentrus azysron*	Predator avoidance	Disruption of GABA-A neurotransmitter receptor in the vertebrate brain by elevated CO_2 and temperature	No	No	Laterality of escape responses found under elevated CO_2	[81,82]
	Gastropods *Dolabrifera razieri* *Bembicium nanum* *Siphonaria denticulate*	Developmental rate and embryonic mortality	Unknown	No	No	Developmental rate and embryonic mortality negatively affected by stressors (UV, salinity, and temperature). Importantly, multiple stressors produced dramatically different results than any single stressor	[83]
Habitat disturbance	Killifish *Fundulus heteroclitus*	Metabolism	Decreased sensitivity of the AHR-mediated signaling pathway	Yes	Yes	Multiple populations from polluted sites independently evolved alterations in the same developmental pathway for higher PCB tolerance	[77–79]
	Soapberry bug *Jadera haematoloma*	Feeding morphology (‘beak’)	One significant QTL found for ‘beak’ length and three for body size	Yes	Yes	Invasive tree species have created a novel host for soapberry bugs which diverged into ecomorphs based on feeding morphology adapted to the different fruit of their native and invasive hosts	[80,81]
	House finches *Carpodacus mexicanus*	Bone development, beak morphology	Earlier and elevated levels of BMPs	Yes	Yes	Differences in bill development between rural and urban populations with earlier and higher levels of BMPs in urban environments	[76]
Invasive species	Chinese tallow tree *Sapium sebiferum*	Mass, leaf area	Unknown	Yes Increased plasticity	Yes	Introduced trees show increased plasticity in leaf biomass and leaf area in response to different light regimes	[84]
	Purple loosestrife *Lythrum salicaria*	Shoot biomass	Unknown	Yes Increased plasticity	Yes?	Invasive plants show increased plasticity in above-ground biomass in response to water and nutrient conditions compared to native species	[44]
	Periwinkle *Littorina obtusata*	Shell thickness	Unknown	Yes Decreased plasticity	Yes	Snails exhibited decreased plasticity in shell thickness in response to invasive crab species	[85,86]
	Pumpkinseed sunfish *Lepomis gibbosus*	Body and trophic morphology	Unknown	Unknown	Yes	Invasive populations in Europe have decreased morphological plasticity compared to native populations	[87]

[a] These threats were split into climate change, habitat disturbance, and invasive species, although these topics include a degree of overlap. Where possible we state the developmental mechanism responsible for the change as well as if there was a change at the level of phenotypic plasticity, whether this change was adaptive or maladaptive, and whether or not genetic variation was shown to underlie this plasticity.

Box 2. Awareness of Development Aids Conservation: A Sea Turtle Example

A strong example of how developmental knowledge benefits conservation can be found within sea turtle conservation efforts. Knowledge of developmental plasticity has directly aided conservation because eggs (and thus the early stages of development) are often artificially reared to protect offspring from predation. It is now well known that temperature plays a strong role in sex determination through early stages of sea turtle development, but during the 1980s conservation practices were inadvertently skewing sex-ratios by keeping all eggs at the same temperature [88]. This has since been mitigated in conservation practices that vary nest and or rearing temperatures to balance sex ratios. Additional phenotypes such as locomotor ability have also more recently been shown to be affected by temperature (Figure IA) [89–91]. These traits include crawling speed and the ability to 'self-right' when a turtle is overturned, and are important for predator avoidance post-hatch when nestlings make their brief journey across land to the ocean (Figure IB) [92] (photos courtesy of Gustavo Stahelin). Conservation programs for sea turtles are now being fine-tuned to take on this newer knowledge of thermal plasticity to vary incubation temperatures and ultimately enhance survival through improved predator avoidance [88,93]. Overall, this example suggests that other threatened species could benefit from the incorporation of developmental knowledge into conservation programs.



Trends in Ecology & Evolution

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(Box 2 gives a case study where developmental knowledge has benefited conservation). However, recent suggestions to advance conservation involve targeted gene flow, whereby adaptive alleles are introduced into populations, or even direct genetic manipulation to introduce genetic variation into populations [20]. While such approaches are still being debated, and will need considerable care before even considering their implementation (especially because the G–P map is determined by environmental conditions), evo-devo offers an inroad into understanding the direct causation for phenotypic change. This could provide robust information needed for conservation issues (i.e., identifiable molecular units of conservation), and perhaps even evidence for legal proceedings [21,22]. Therefore, we next outline some of the major concepts and research areas that currently drive the field of evo-devo, and discuss how they can apply to conservation.

Evolvability: A Central Focus of Evo-Devo Aligns with Conservation

Evolvability has become a key conceptual focus for evo-devo research [23]. While evolvability has a range of definitions in the literature, all focus on the idea of evolutionary potential, and what generates it [24]. However, we consider here evolvability as the ability of a population to produce adaptive genetic variation [25]. Meanwhile, theory suggests that conservation should seek to preserve the adaptive potential of populations for evolution to proceed and populations to persist [26]. Conservation practice has made efforts toward this by focusing on maintaining higher levels of additive genetic variance (e.g., captive breeding programs, protection of evolutionary significant units). Therefore, evolvability research somewhat aligns with conservation theory but it places focus on variation that is distinct from shear amounts of heritability (i.e., the additive genetic variance of a population). Thus, empirical evolvability research aimed at understanding adaptive G–P interactions (and how they develop) could provide approaches for more precise conservation targets (i.e., the variation that is involved in the evolution of adaptation).

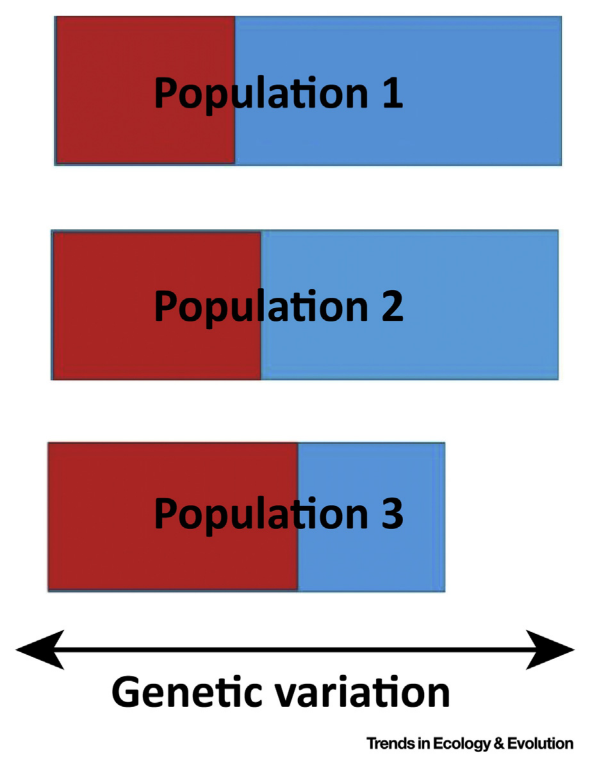
Evolvability research can include investigating molecular genetic mechanisms that differ between phenotypes, how the environment contributes to variation at the phenotypic level, and what biases phenotypic variation along specific evolutionary trajectories. Thus, evolvability is a powerful framework that could help conservationists to understand how evolution occurs from a perspective that targets the most salient features of a population. For example, conservation biology prioritizes adaptive evolutionary potential – a practice synonymous with preserving evolvability. However, the empirical practice of conservation genetics often focuses on identifying and comparing total levels of neutral genetic variation without directly investigating its adaptive potential [27]. For example, genomic approaches have recently transformed conservation by identifying genomic evidence of inbreeding depression, enhanced estimations of effective population size and migration rates, and the identification of allele frequency differences between locally adapted populations [4]. However, while some results may point toward adaptive variation, the functions of such loci are rarely investigated. This is especially problematic because relationships between neutral and adaptive diversity are at best weakly related [28,29]. Unfortunately, this approach does not recognize the changing function of genes over the course of development, environments, or genetic backgrounds (Box 3). More direct functional investigation could provide vital information for more effective decisions. For example, investments in the translocation of individuals to maintain gene flow between fragmented populations have sometimes actually worsened declines [30–33]. Indeed, information at a more mechanistic level could inform us about such risks as outbreeding depression, which likely explains these worsened declines.

Phenotypic Plasticity and Conservation

While anthropogenic effects on the environment can rapidly change selection regimes for populations (causing contemporary evolution), they also simultaneously impact on developmental conditions (inducing plastic responses) (Boxes 1,4). This means that the widely recognized phenomenon of contemporary evolution, which has impacted on conservation biology, could be due in part to (i) changes in the G–P map via **phenotypic plasticity**, and (ii) subsequent selection on genetic variation exposed in the phenotype by environmental change [34,35]. Taken together, this means that predicting the evolution of populations to future environments is difficult without recognition of plasticity by conservationists. We outline here several areas where awareness of plasticity could inform conservation.

Box 3. Evolvability as a Conservation Tool

The concept of evolvability could be applied to enhance the efficiency of current conservation genetic strategies. The focus on sheer amounts of molecular genetic variation may overlook populations with greater evolutionary potential. Rectangles in Figure I represent hypothetical populations possessing different ratios of adaptive (red) and neutral (blue) genetic variation. Population 3 exhibits relatively lower total levels of genetic variation but a higher degree of adaptive evolutionary potential (i.e., evolvability). Population 2 exhibits a greater degree of adaptive genetic variation than population 1 but equal total levels of genetic variation. Current practices would wrongly prioritize populations 1 or 2 equally because they are based on overall levels of genetic variation, and not on the greatest degree of adaptive potential (possessed by population 3).



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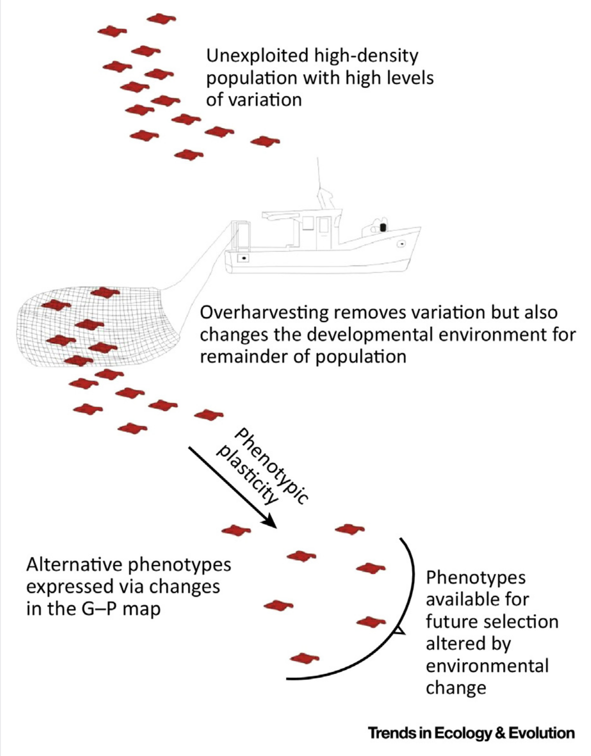
Plasticity closely accompanies the broader idea of evolvability in evo-devo and has been studied for its ability to provide novel adaptive variation [13]. Of relevance to conservation would be the core theoretical ideas of plasticity research suggesting that it can allow populations to persist and quickly adapt to novel environmental conditions [36–38]. One interpretation suggests that plasticity could lessen the impact of natural selection on adaptive genetic divergence through the rapid phenotypic change it allows without a requirement for genetic change. Compounding this, such rapid phenotypic change can also allow dispersers to adapt to a variety of environments, facilitating gene flow between subpopulations and preventing local adaptation [36].

However, theory and emerging data suggests that plasticity should be selectively favored in novel or fluctuating environments [39–42] – a situation likely experienced by an introduced species or a population living within a damaged habitat. Heritable variation in plasticity has been widely demonstrated and has played a role in at least some species invasions. For example, head size plasticity has decreased over contemporary time within introduced populations of

Box 4. Evo-Devo and Fisheries-Induced Evolution (FIE)

An example of how evo-devo can be used to understand FIE. Conventional Darwinian theory is limited to the idea that variation is removed from a population during overharvesting, thus causing evolutionary change. This is the prevalent view of how changes in life-history traits such as age and size of maturation have occurred in FIE. However, the act of overharvesting can cause a multitude of changes, such as a reduction in population density. This would essentially change the developmental environment for the remainder of the population and induce plastic responses. For example, a reduced density would probably have a significant effect on the social environment to which juveniles are exposed. Social isolation in fish has been shown to reduce schooling tendencies and increase aggression among individuals [94–96]. While a reduced population density may provide a greater number of prey per individual, foraging may be reduced due to lack of social interaction. This could alter the G–P map and ultimately change the genetic basis of FIE (Figure I).



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tiger snakes (*Notechis scutatus*) relative to ancestral populations [43]. This rapid adaptive shift from phenotypically plastic expression to developmental canalization suggests that plasticity could initiate species invasions by allowing invaders to persist in a novel environment [44]. In addition, because plasticity itself can evolve extremely fast [40], initial responses to anthropogenic disturbances could influence longer-term evolution well after a disturbance has been mitigated (Box 4).

Heritable variation in magnitudes of plasticity can be important for determining the response of both invasive and native populations (Table 1). For example, invasive purple loosestrife (*Lythrum salicaria*) was found to exhibit increased levels of plasticity in above-ground biomass relative to native populations in response to variation in water and nutrient conditions [45]. Similarly, populations of marine snails (*Littorina obtusata*) demonstrate changes in the magnitude of shell thickness plasticity in response to an invasive predatory crab species (*Carcinus maenas*) that corresponds with invasion history (i.e., newly exposed snails were more plastic) [46]. Such evolutionary responses in plasticity may be widespread but not apparent to conservationists because they require laboratory experiments to demonstrate their existence. Thus, plasticity is likely to be relevant for broad disturbances where responses have been documented but actual evolutionary changes have only been assumed [12].

Plasticity may actually 'hide' the impact of anthropogenic effects because it can compensate for less than ideal environmental variation and buffer the phenotype. These responses can manifest themselves in a phenomenon known as countergradient variation whereby the genotype becomes decoupled from a constant phenotype [47]. This phenomenon is revealed through common-garden experiments that show enhanced phenotypic differences between populations relative to their natural environments where conditions vary [47–49]. Such developmental adjustments could pose a major problem for conservation because evolutionary change (via the evolution of plasticity) and the loss of genetic variation are made difficult to detect. For example, fishing stocks could be identified as a single stock based on similar external features, when in fact a very different developmental strategy has been employed to achieve the same phenotype [49]. Thus, countergradient variation (by decoupling G–P relationships) may mislead researchers to believe that a great deal of genetic variation between phenotypically similar populations is neutral when it could actually maintain compensatory mechanisms. We are unaware of conservation practices that employ knowledge of countergradient variation probably because it is by nature not obvious, raising the possibility it may be much more common than we are currently aware.

Phenotypic plasticity highlights the impact that the environment can have upon development, but this relationship may not be unidirectional. Specifically, **niche construction** theory has recently gained increased attention and refers to the ability of organisms to alter the environment they (and other organisms) experience [50–52]. Thus, organismal development itself can provide ecological feedback that determines phenotypic outcomes (i.e., 'developmental niche construction') [53] (Box 1). Thus, plastic responses can have broad impacts throughout a community, with alterations of its ecological dynamics being well underway before demographic and genetic change has occurred. Taken together, the findings and ideas above suggest how consideration of plasticity as a mechanism for broader ecological change, buffer of environmental stress, and trait under selection would benefit conservation.

Phenotypic Integration and Modularity in Conservation

Responses to anthropogenic disturbance tend to be studied in the context of one or two traits. However, it should be expected that responses would likely extend across an entire complement of traits that impact on fitness [54]. Therefore, an understanding of such phenomena would be aided by the concepts of **phenotypic integration** and modularity, another focus of research within evo-devo [55,56]. Phenotypic integration refers to correlations among traits, while the related concept of modularity is more specific and suggests that correlations among traits can occur in smaller subsets in an organism. Reasons for phenotypic integration and modularity can vary, such as where an adaptive response for one trait may conflict with the adaptive responses of other traits, or where there are underlying developmental processes that tightly link traits together [56]. Recent research suggests that evolvability is in part determined by integration among traits, and is highest in cases where integration is moderate rather than extremely strong or weak [55,57]. This is because strong integration can bias evolutionary responses to a limited range of trajectories, while weak integration may slow the accumulation of adaptations [55]. Thus, integration measures could provide an additional means of assessing evolutionary potential in disturbed populations and complement current assessments of biodiversity.

Phenotypic integration is relevant to conservation because it can change quickly in response to environmental conditions [58] (Figure 1). While patterns of phenotypic integration can themselves evolve [56], specific types of integration may also be prevented through anthropogenic disturbances. For example, endocrine disruptors are chemical pollutants (e.g., pharmaceuticals, dioxins, pesticides) that can interfere with hormonal functions and ultimately developmental processes [13]. Endocrine disruptors work by mimicking naturally occurring hormones, often binding to receptors and blocking the endogenous hormone from binding. Hormones are vital for integration because they coordinate the coexpression of behavioral, physiological, and morphological traits to allow them to function together [59]. The ability of one hormone signal to interact with multiple targets to influence multiple traits has been referred to as hormonal pleiotropy, and the correlations among traits mediated by the same hormone as hormonal correlations [60–66]. Such hormonally based patterns of integration would likely be especially disturbed by endocrine disruptors because the sensitivity of different target tissues can vary. Similarly, hormone signals are naturally not only secreted at varying levels in varying temporal patterns, they are also broken down at differing rates, transported by carrier proteins in ways that make them unavailable to the target, and often are metabolized into new active forms at the target [59,67]. Therefore, a habitat polluted by hormone mimics could significantly alter phenotypic integration during development, leading to reduced fitness or altered responses to an environmental disturbance.

Because phenotypic integration can bias and therefore inform predictions for future evolution, it should be applicable for several conservation problems. For example, phenotypic integration may be especially useful for understanding species invasions where phenotypes are known to differ at the leading edge, versus the initial invasion sites. It has been shown that cane toads (*Rhinella marina*) on the leading edge of the invasion in Australia are larger and have relatively longer legs than those in the already colonized areas [68]. This increase in leg length has subsequently been shown to correlate with an increase in the occurrence of spinal arthritis [69] (Figure 1). This suggests that a breakdown of adaptive patterns of integration is occurring between the legs and spine, perhaps suggesting an unstable phenotypic state where normally detrimental trade-offs are actually favored at the invasion edge. New statistical advances are now making it possible to directly investigate how integration and modularity relate to fitness in populations, as well as their genetic basis [56,70,71]. Thus the application of 'integration thinking' from evo-devo can move toward an increasingly viable tool for conservation.

Mechanistic Evo-Devo and Conservation

Evo-devo emerged in part with the insight that many molecular pathways are functionally conserved across broad phylogenetic scales [72]. This knowledge has made it possible for organisms beyond standard laboratory models to be investigated to understand gene function in a broad range of taxa [16,73]. However, conservation biology rarely overlaps with **functional genetics** and focuses on projection models that integrate demographic processes such as migration and population size [73,74]. Nonetheless, conservation is currently benefitting from genomic advances which enable identification of the precise molecular changes impacted by anthropogenic influences. Specifically, these modern techniques could be used to identify signaling pathways affected by anthropogenic disturbances to directly inform functional genetic studies. Indeed, changes in members of the molecular network underlying wing development (*En*, *Ubx*, *Cut*, *Exd*, *Ph3*, and *Mef2*) in multiple populations of an ant species (*Monomorium emersoni*) have consistently affected their wing phenotype, life history, and dispersion abilities in response to natural climate change over the past 80 000 years [73]. Such integration of the responses of molecular pathways with environmental changes could be used to build projection models to predict species distributions under future climate change scenarios. Determining the specific genetic mechanisms of conservation concern could even expand functional genetics (in the context of evo-devo) beyond the typical examination of early developmental processes to broader ontogenetic timescales where anthropogenic effects may be most relevant. This could enlighten both evo-devo and conservation, with such approaches becoming increasingly feasible and precise for non-model organisms [16,75].

Indeed, the developmental genetic basis of responses to human disturbances are beginning to be more directly investigated. For example, house finches (*Haemorhous mexicanus*) inhabiting both urban and rural habitats display adaptive divergence related to bite force and bill morphology because urban populations feed more frequently on hard seeds [76] (Figure 1). Notably, the developmental basis of this divergence (increased bill size in urban finches) is associated with changes in the expression of bone morphogenetic proteins (BMPs). BMPs are expressed earlier and at higher levels in the mandibular primordia in urban finches (with stronger bite force) than rural populations [76]. Similarly, the precise mechanistic basis of adaptation to environments contaminated with toxins has been determined for the Atlantic killifish (*Fundulus heteroclitus*) [77]. Specifically, populations exposed to pollutants have independently converged on reduced signaling in the aryl hydrocarbon receptor (AHR) pathway which metabolizes hydrocarbon pollutants such as polychlorinated biphenyls (PCBs) to elicit toxic effects [77–79]. Finally, the genetic basis of evolutionary responses by soapberry bugs (genus *Jadera*) in relation to invasive host trees has been investigated. On the Florida peninsula, populations of *J. haematoloma* now feed on the seeds of both the native balloon vine (*Cardiospermum corindum*) and the invasive Chinese flametree (*Koelreuteria elegans*) which was introduced into urban areas about 70 years ago. These populations show ongoing rapid evolution of their mouthparts (stylets or 'beaks') and body size to better match the seed defense structures of newly introduced hosts [80]. Quantitative trait locus (QTL) analysis has recently revealed a genomic region related to beak length, and three regions related to body size [81]. While rare, such mechanistic investigations show that determining the precise basis of anthropogenically driven changes is possible. The task now is to expand such approaches and implement their findings into conservation decisions.

Concluding Remarks

Conservation biology is continually improving with technical advances and a greater focus on preserving the evolutionary process (e.g., guidelines for Sites of Special Scientific Interest in the UK). However, we suggest that evo-devo could offer a step-change in how conservation approaches problems (Box 5). By considering the dynamics of phenotypic development and an explicit focus on sources of variation, conservation could directly embrace the realities of populations living in changing environments. While this will be difficult to implement in some systems, we contend that most systems will be amenable, as demonstrated by the wide range of examples above. In addition, if a particular species proves to be difficult, investigations into gene function (or the response to an environmental stressor) identified from a field survey of allelic variation can be tested in surrogate model species. This would provide better-informed reasons for targeting the preservation of particular types of allelic variation. Although less direct, this can also provide functional genetic approaches that are feasible for a wide range of species that cannot be readily bred, have a long life-history, or are generally not amenable to laboratory conditions. Thus, evo-devo has much to offer conservation biologists, especially when trying to predict future evolutionary responses. However, it should also be noted that evo-devo itself could advance by cooperating with conservation. Being a relatively new field emerging in part from the mechanistic perspective of developmental biology, evo-devo carries a general legacy of 'typological thinking' [16]. A conservation context would further promote a more population-based approach for evo-devo with the potential to discover the underlying genetic and environmental basis of complex phenotypes. This would be useful for further broadening of evo-devo within the wider realm of evolutionary biology.

Outstanding Questions

We have discussed the potential for integration between conservation biology and evo-devo. This is a new approach and therefore a number of outstanding questions are raised. Addressing these could serve as a way forward for both the field of evo-devo and conservation biology.

Can developmental responses serve as monitoring tools that provide an 'early warning' prior to demographic and genetic change?

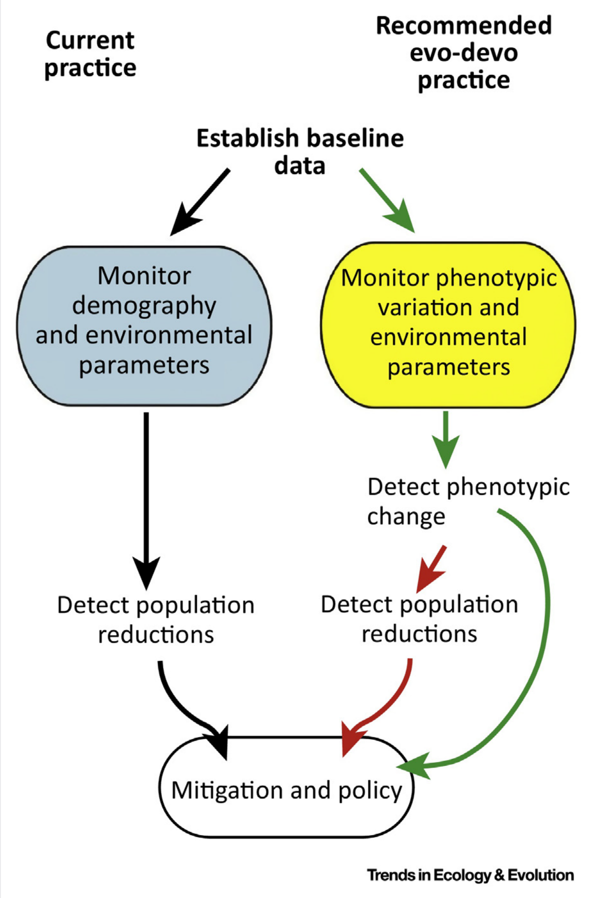
Can we effectively incorporate an understanding from lab-based developmental biology experiments into the wider scale of nature? If so, should we prioritize species for conservation that are identified as having the highest evolutionary potential?

To what extent does phenotypic plasticity allow organisms to persist in the face of anthropogenic changes to environments?

How widespread is counter gradient variation and what environmental conditions could it be masking from detection?

Box 5. Future Directions

Conservation can be enhanced by the addition of 'developmentally minded' approaches. We provide here a schematic to generally contrast how our evo-devo-based recommendations (right) integrate with current conservation practices (left). In many instances conservation issues are recognized as changes from some form of baseline data, such as population density or environmental variables. For the evo-devo approach, baseline phenotypic or genomic data could also be obtained from undisturbed habitats or historical museum samples. This addition to existing practices has better potential to identify phenotypic changes relatively early as a population responds to a stressor. It will not always be possible to recognize that some phenotypic changes represent a threat that precedes demographic changes (red arrows). However, in many cases such retrospective information may enable conservationists to determine the causative environmental stressor. Thus, developmental monitoring could serve as an 'early warning' for other systems facing threats (Figure I). Q17



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Q7 Therefore, toward the benefit of future biodiversity we are hopeful that practitioners investigating the origins of variation can increasingly collaborate with those who manage and conserve it.

Q8 Uncited references

[97,98].

Acknowledgments

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Supplemental Information

Supplemental information associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.tree.2017.07.002.

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