

Meta-analysis at the intersection of evolutionary ecology and conservation

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Abstract We review the use and findings of meta-analyses that link evolution to conservation. An initial search of the literature produced 606 studies that appeared to be relevant, 120 of which proved to be narrow-sense meta-analyses. Only 23 explicitly intersected evolution and conservation. Collectively these meta-analyses summarized the results of some 2,000 studies of ~3,000 species. Most of the meta-analyses examined questions such as links between genetic variation and fitness of individuals in small populations, genetic consequences of habitat fragmentation, and changes in traits in time and space in response to a variety of human impacts ranging from pollution to invasive species and climate change. By summarizing the results of large numbers of disparate studies, meta-analyses usually confirmed theoretical expectations, but sometimes revealed that predicted relationships or differences are much weaker than conventionally assumed. They have also been helpful in pointing out benefits and pitfalls of alternative methodologies and metrics. Other major areas of conservation concern such as impacts of over-exploitation have been synthesized in other ways, but not yet by formal meta-analyses. We conclude that most of the meta-analyses that have been done so far are aimed more strongly toward advancing our understanding of evolution than of conservation. We remain hopeful that this tool will find increasing use in new questions at the intersection of these fields, and be aimed more directly at providing diagnoses and prescriptions for action in the field of conservation management.

Keywords Conservation genetics · Contemporary evolution · Extinction · Human-induced change · Systematic reviews

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Introduction

It has been some 20 years since meta-analysis was imported from medicine and the social sciences into ecology and evolutionary biology (Gurevitch et al. 1992; Vanderwerf 1992). The use of these techniques for synthesising studies has grown exponentially since then (Stewart 2010). The adoption of meta-analysis in ecological fields coincided with, and undoubtedly fuelled, a growing scientific appetite for pulling results together to make geographically or taxonomically broad-scale comparisons. In the field of biodiversity conservation, many of the greatest hits in high-flying journals have been global syntheses, particularly in recent years. Some of these have been systematic reviews, which have led to striking geographic maps of biodiversity distribution or of human impacts used to support qualitative conclusions (e.g., Worm et al. 2006; Halpern et al. 2008), while others have consisted of formal meta-analyses (Gardner et al. 2003; Gibson et al. 2011). Influential institutions (e.g., the National Center for Ecological Analysis and Synthesis in the USA, and the Centre for Evidence-Based Conservation in the UK) have actively promoted the use of systematic reviews and meta-analysis in applied ecological fields, with the latter launching a peer-reviewed journal (*Environmental Evidence*) dedicated to applied ecological syntheses.

At the same time that meta-analysis has been spreading across the ecological landscape, there has been a separate push to ask how evolutionary ecology may be relevant to pressing conservation issues of the day (e.g., Stockwell et al. 2003; Ferrière et al. 2004; Carroll and Fox 2008; Höglund 2009). The potential importance of genetic variation for population persistence, recognized early by Soulé and Wilcox (1980) and Soulé (1986, 1987), was initially downplayed by theoretical models suggesting that demographic effects should play a much greater and immediate role in extinction (e.g., Lande 1988). But it is clear that many anthropogenic activities are changing the magnitude, direction and very nature of selection pressures on wild populations, and evidence is mounting that phenotypic change is occurring, sometimes very quickly, in human-altered environments (reviewed by Palumbi 2001; Hendry et al. 2008; Smith and Bernatchez 2007; Darimont et al. 2009). Given that many human activities (e.g., logging, fishing, animal and plant domestication, and species introductions) have been occurring over timescales that far exceed the time needed for contemporary evolution (*sensu* Stockwell et al. 2003), we can expect that evolutionary processes play a part in shaping today's wild populations. Given the ever increasing number of studies linking conservation and evolution, and the fact that meta-analysis has infiltrated both evolutionary and applied ecology, it is timely to ask how important meta-analytical techniques have been in contributing towards syntheses at the intersection of these two disciplines.

In this review, our goal is to appraise what meta-analyses have and have not done to enhance our understanding of the contribution of evolutionary ecology toward diagnoses and prescriptions for action in the field of conservation management. First, we summarize the number of studies that are relevant to this synthesis. We then present the major findings of these studies and ask how they have advanced the field. We conclude with some thoughts about what meta-analyses have and have not accomplished, and what future contributions they might make.

Evolutionary conservation meta-analyses: common occurrence or rare breed?

We searched a large database (ISI Web of Science, 2011 Thomson Reuters; year span: 1899–2012) to extract published meta-analyses relating to evolutionary aspects of

conservation. We restricted our search to relevant journals (i.e., only biosciences, excluding medical journals). The keywords used to capture meta-analysis, conservation and evolution are given in Table 1, and the results for combinations of these search terms are shown in Fig. 1. The keywords for conservation (Table 1) were designed to target the most important human activities responsible for contemporary extinctions: over-exploitation ('exploit*', 'fisheries', 'fishing', 'hunting', 'logging', 'forestry', 'harvest*'), habitat fragmentation or degradation ('habitat', 'pollution', 'fragment*', 'contamina*', 'inbre*', 'founder*', 'restor*', 'UV'), and exotic species ('invas*', 'exotic*', 'alien*', 'introduc*'). We also searched for studies of climate change ('climate change', 'warm*', 'acidif*'). Finally, we added 'ecology' as a search term to ensure the capture of applied ecological meta-analyses that had an evolutionary angle which were overlooked by the use of the above search terms in their title, abstract or keywords.

Our search was, by necessity, incomplete. It was limited to papers written in English and published in journals (and some books and conference proceedings) included in the Web of Science. However, since our goal was not to produce an exhaustive list of meta-analyses in evolutionary conservation, but an overview to understand the types of topics tackled to date, we believe that our strategy was adequate.

It is immediately apparent that meta-analysis, at least as a keyword, has been widely adopted in the separate fields of ecology, evolution and conservation (Fig. 1). Some 75 papers have been published annually, on average, since the first ecological meta-analysis, with the rate increasing over time (see also Stewart 2010). At first glance, meta-analyses at the intersection of conservation and eco-evolution are less frequent, but nonetheless not unusual (Fig. 1).

However, closer inspection of these cross-disciplinary papers reveals that the term 'meta-analysis' has been applied broadly to any analysis that includes data from multiple sites, species, and/or sources, regardless of the nature of the response variables considered or the analytical procedure used. For this paper, we view meta-analysis strictly as the combining of effect sizes (i.e., scale-independent measures of the magnitude of an effect of interest, which can be meaningfully compared across studies), weighted to reflect their statistical robustness (often by the inverse of the study variance), into a global effect size. Uncertainty around this global effect size can then be understood by examining the effect of relevant moderators. Classical meta-analytical methods have been described by Hedges and Olkin (1980) and Hunter and Schmidt (1990). More recently, Bayesian meta-analytical methods have been developed, but these are still variations on the original, *sensu stricto* meta-analysis and we include them here. In another paper in this special issue on meta-analyses, Nakagawa and Santos (2012) review the different forms of meta-analysis and

Table 1 Keywords used in Web of Knowledge searches. The generic terms are those used in Fig. 1. Within each generic term, the search terms were linked by "or"

Generic term	Search terms
Meta-analysis	Meta-anal*or metaanal*
Ecology	Ecol*
Evolution	Evol*or select*
Conservation	Conservation, exploit*, fisheries, fishing, hunting, logging, forestry, harvest*, habitat, pollution, fragment*, contamina*, inbre*, founder*, restor*, UV, invas*, exotic*, alien*, introduc, climate change, warm*, acidif*

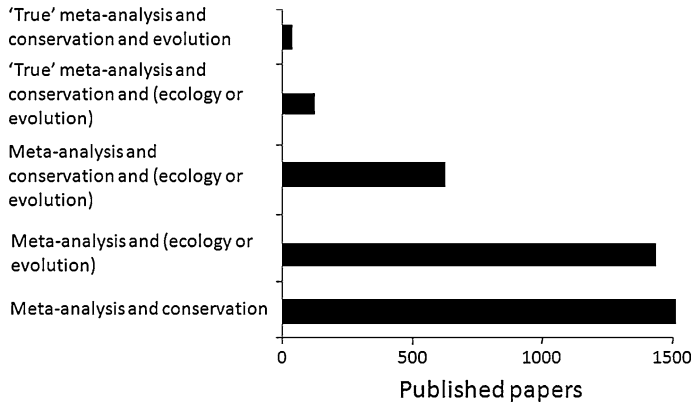


Fig. 1 Number of published papers yielded by searches using various combinations of search terms related to meta-analysis, evolutionary ecology and conservation. A full description of the search terms is given in Table 1

how they relate to one another, including those that consider phylogenetic relationships among species (see also Jennions et al. 2012).

When we removed studies that performed weighted analyses on response variables that are clearly not effect sizes, and those that used meta-analysis to combine the results from multiple sites used in a single field experiment, fewer than 20 % (120/606) of the studies remained. Of these narrow-sense meta-analyses, only 23 dealt with a conservation subject from an explicitly evolutionary perspective (Table 2). This last cut was difficult. We considered as relevant only those studies which were presented and interpreted in an evolutionary framework by the authors. For example, the same study showing different impacts of native and introduced herbivores on exotic plants could be framed as a purely ecological question (in which case it would have been excluded), or framed in the context of the effect of co-evolutionary history on invasions (in which case, it would have been included). We chose not to recast the authors' emphases to allow for clearer selection criteria.

Meta-analytical insights into evolutionary aspects of conservation issues

The 23 evolutionary conservation meta-analyses fell into four general subject areas: relationships between genetic diversity, traits and fitness; small population size; changes over time; and local adaptation (Table 2). We review briefly each of these subjects and highlight the contributions, if any, of meta-analysis to clarifying issues and generating new ideas.

Genetic diversity, traits and fitness

Genetic diversity is believed to be important for conservation because individuals with low levels of genetic variability, owing to inbreeding or genetic drift, may have lower fitness. Reduced reproductive success or survival may be due to the expression of deleterious recessive alleles, the loss of heterozygote advantage, or both (Charlesworth and Charlesworth 1987, 1999). Impairment of individual fitness may lead to a higher extinction risk of

Table 2 Published meta-analyses of evolutionary aspects of conservation. For each source, the maximum number of studies and species are given; some analyses have more or fewer comparisons according to missing data or multiple comparisons per species

Source	Subject	Sample sizes
Genetic diversity, traits and fitness		
Møller (1999)	Asymmetry as a predictor of growth, fecundity and survival	29+ studies, 23+ species
Reed and Frankham (2001)	Molecular versus quantitative measures of genetic variation	42 studies, >49 species
Coltman and Slate (2003)	Correlations between phenotypic and genetic variation	22 studies, 23 species
Reed and Frankham (2003)	Correlation between fitness and genetic diversity in various taxa	24 studies, 21 species
Leimu et al. (2006)	Relationships between plant population size, fitness and genetic variation	14–45 studies, 12–41 species
Chapman et al. (2009)	Correlations between fitness and heterozygosity in various animal taxa	65 studies, 60 species
Small population sizes		
Byers and Waller (1999)	Purging genetic load: comparisons among plants	11 studies, 45 populations
Črnokrak and Barrett (2002)	Purging genetic load: experimental evidence from various taxa	28 studies, 22 species
Aguilar et al. (2008)	Genetic consequences of habitat fragmentation in plant populations	101 studies, 102 species
Honnay et al. (2008)	Role of seed banks in maintaining genetic variation	42 studies, 42 species
Angeloni et al. (2011)	Population size, life history and inbreeding depression in plants	116 studies, 107 species
Uller and Leimu (2011)	Founder events and changes in genetic diversity in plants and animals	87 studies, 85 species
Changes over time		
Gienapp et al. (2007)	Changes in avian migration timing	18 studies, 249 species
Hawkes (2007)	Invasive plant initial advantages and enemy release over time	62 studies, 67 species
Petrin et al. (2008)	Contrasts between anthropogenic and natural acidity of streams	60 studies, multiple aquatic invertebrates
Gardner et al. (2009)	Shifting latitudinal clines in avian body size related to global warming	517 specimens, 8 species
Crispo et al. (2010)	Evolution of phenotypic plasticity in response to human disturbance	20 studies, 20 species
Zvereva and Kozlov (2010)	Response of terrestrial arthropods to point sources of pollution	134 studies, 448 comparisons
Kozlov and Zvereva (2011)	Response of plants, fungi, arthropods to aerial pollution	~ 500 studies, 1,095 comparisons

Table 2 continued

Source	Subject	Sample sizes
Doorduyn and Vrieling (2011)	Invasive plant evolution of chemical defence	15 studies, 9 species
Munguia-Rosas et al. (2011)	Selection on flowering time	296 studies, 86 species
Local adaptation		
McClelland and Naish (2007)	Fitness outcomes of crossing unrelated fish populations	34 studies, 670 comparisons
Leimu and Fischer (2008)	Local adaptation in plants revealed by reciprocal transplants	35 studies, 32 species
Fraser et al. (2011)	Local adaptation in salmonid fishes based on interpopulation	15 studies, 13 species comparisons

populations, and in the longer term, lower genetic diversity may result in a reduced potential of populations to adapt to changing conditions.

Early qualitative reviews suggested that inbreeding was prevalent and that its cost in terms of survival was high, at least for captive populations (e.g. Ralls et al. 1979). There was more debate about whether this was also the case in wild populations, although again qualitative reviews concluded that inbreeding and inbreeding depression were both more the rule than the exception (Frankham 1995; Crnokrak and Roff 1999). Simplistically put, because inbreeding depression is directly related to the inbreeding coefficient F , which reflects the amount of genetic variation present (Falconer and MacKay 1996), it follows that genetic variation in a population, and by extension in individuals, should correlate with current fitness, or with traits that potentially reflect fitness, but how strong this correlation should be is not clearly predicted by theory.

Five formal meta-analyses have been carried out to measure the strength of heterozygosity-fitness correlations (HFCs) and understand sources of variation in these relationships (Table 2). Some of their results are summarized in Fig. 2. Most meta-analyses compared several metrics of genetic variation. The two most often considered were multi-locus heterozygosity (MLH)—the proportion of heterozygous loci within an individual, based on allozyme or microsatellite data—and mean d^2 —the squared difference in lengths of repeats between two alleles at a locus, averaged over all loci examined (Fig. 2).

All meta-analyses found significant positive correlations between genetic variation and fitness. However, the magnitude of the overall relationships was highly variable among meta-studies. If an effect magnitude of $r = 0.1$ is considered small, $r = 0.3$ is considered medium, and $r = 0.5$ is considered large (Cohen 1988), then the overall effect sizes reported varied from very small to medium. Much heterogeneity among studies was reported in most cases, and the identified sources of variation included heterozygosity metrics (i.e., MLH tends to have a higher HFC than other metrics), fitness components (i.e., life-history traits sometimes have higher HFCs than morphological traits), and taxon characteristics, such as plant mating system (Leimu et al. 2006).

There are two striking patterns in Fig. 2. The first is the apparent association between sample size and overall effect size, with the two largest studies posting the smallest effect sizes. The very large sample sizes were obtained because there were more studies

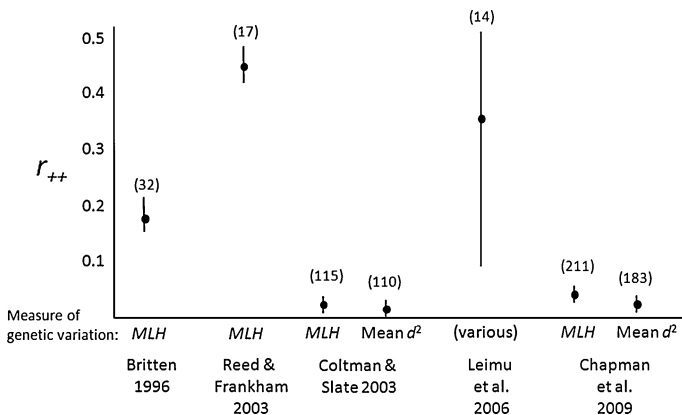


Fig. 2 Comparison of overall effect sizes (r_{++} , with 95% confidence intervals) measuring the strength of the relationship between various measures of genetic variation and fitness obtained in five published meta-analyses. Sample sizes (number of relationships) are given in parentheses

available, and also because more effect sizes were extracted per study in later than in earlier meta-analyses. However, analyses based on study averages did not raise the overall effect sizes substantially (Coltman and Slate 2003; Chapman et al. 2009). One potential important difference in data between smaller and larger meta-analyses is that the former are based largely on allozyme variation, while the latter are based on microsatellites. However, Leimu et al. (2006) found, albeit with small sample sizes, that DNA-based estimates of genetic variation yielded significantly *stronger* HFCs than allozyme-based estimates, so the source of data used to estimate genetic variation might not be the sole answer.

The second notable feature of Fig. 2 is the very large confidence interval in the study by Leimu et al. (2006). This study focussed solely on plants while all others focussed on either animals or a combination of plants and animals. Plants are perhaps more variable in their HFCs than animals, although why this should be is not clear. Leimu et al. did have a small sample and combined at least five metrics of genetic variation into the overall analysis, both of which could have generated particularly large variation.

These meta-analytical studies confirmed the conclusions of earlier qualitative reviews: genetic variation and fitness are linked. Meta-analyses went one step further than the qualitative reviews by providing estimates of the strength of this association. In spite of some differences, meta-analyses have clearly established that heterozygosity—fitness correlations are widespread but generally weak, leading to conclusions ranging from good support for theory because of the significant positive HFC (Reed and Frankham 2003; Leimu et al. 2006) to little or no support because of the small effect sizes found (Britten 1996; Coltman and Slate 2003; Chapman et al. 2009). A clearer synthesis of the sources of variation in HFCs is still needed.

Small population sizes

Small population sizes are intimately linked with the issues of inbreeding discussed above. Thus, in addition to the obvious concerns about the inherent vulnerability of small populations to extinction due to demographic processes, individual fitness may be weakened by inbreeding depression, which may scale up to increases in risk of population extinction (Wright 1977; Charlesworth and Charlesworth 1987). On a more positive note, it is also possible that natural selection in inbred populations could purge deleterious alleles when they appear in homozygous states, especially if the alleles have large effects (Lande and Schemske 1985; Hedrick 1994). Thus, populations might go through an initial dip in fitness when inbreeding first occurs, followed by a rebound due to a reduction in frequency of deleterious alleles. Individuals from inbred populations may therefore, counter-intuitively, have higher fitness after a period of time than those from more outbred populations in which purging has not occurred.

The first two studies under the ‘Small population sizes’ heading in Table 2 used meta-analyses to test for evidence that inbred populations purge deleterious alleles. Byers and Waller (1999) restricted their analyses to plants, whereas a later study by Crnokrak and Barrett (2002) considered a larger number of studies of both plants and animals. Plants feature prominently in this field because many species are readily amenable to experimental manipulation of rates of outcrossing or selfing, and researchers can also take advantage of natural variation among populations in this aspect of their mating systems.

Byers and Waller (1999) compiled 52 studies that tested for differences between selfed and outcrossed populations, but were only able to use 11 of them for a formal meta-analysis because they needed a mean value for each trait, as well as a measure of variance

and sample size. It seems astonishing that any of the contributing studies could be published without such basic information, but the lack of these metrics is a common lament among “meta-analysts”. The primary studies either compared differences among closely related species, or between populations within species, or among lineages that differed in history of inbreeding. The results of the meta-analysis, combined with the evidence from other studies, showed that genetic purging did not act consistently among wild populations. The authors therefore urged caution in the use of deliberate inbreeding as a tactic by conservation biologists to get rid of deleterious alleles. Crnokrak and Barrett (2002) found more positive evidence for purging, based on a review of experimental evidence from 13 plant species, five mammals, three insects, and one mollusc. Thus, inbred lines often showed increases in fitness-related traits over time. However, they warned that results were variable and that the answer and interpretation depend on which of three methods researchers used to test for purging, which is an important conclusion from this meta-analysis to guide future research.

Other meta-analyses under the ‘small population’ theme covered more disparate topics (Table 2). These include the genetic consequences of founder events (Uller and Leimu 2011), small populations caused by habitat fragmentation (Aguilar et al. 2008), links between inbreeding depression and population size (Angeloni et al. 2011), and the ability of seed banks to provide a reservoir against genetic drift (Honney et al. 2008). The major findings of all four reviews are largely congruent with theory and with each other in the areas where they overlap, though the stories that flow between them are not all seamless. For example, Aguilar et al. (2008) confirmed the prediction that habitat fragmentation leads to loss of genetic diversity in plants, with losses being most pronounced in fragments that are more than 100 years old. But this is not a perfect fit with Angeloni et al.’s (2011) discovery that inbreeding depression in plants is lowest in smaller populations. Ways can be found to make these findings compatible. For example, Angeloni et al. suggested that genetic purging might occur in small populations, which would lead to lower genetic diversity, and to a match with the fragmentation study of Aguilar et al.

All of the meta-analyses relating to small population issues uncovered considerable unexplained variation among the studies that they analyzed. However, researchers who follow up on them have been given several helpful leads in terms of sensitivity of different metrics, as well as variation among taxa in responses. For example, outcrossing plants, and those that are common or recently rare, appear to be more susceptible to the genetic effects of habitat fragmentation than self-compatible species or species that are naturally rare (Aguilar et al. 2008). Moreover, the magnitude of inbreeding depression depends on which life stage is measured, with the lowest effects at the germination stage, and higher and more variable effects on seed set (Angeloni et al. 2011).

Changes over time under human disturbance

The nine meta-analyses in this category have all explored, and sometimes found, evidence for responses to selection from anthropogenic activities over time. Distinguishing between phenotypic plasticity and true evolutionary change has not been easy for most of them, but the results of many are certainly suggestive. For example, in a meta-analysis of eight passerine birds from south-eastern Australia, Gardner et al. (2009) found strong and consistent reductions in body size that match expectations from effects of warming temperatures. The authors were unable to distinguish conclusively between genetic and purely phenotypic changes, but several lines of circumstantial evidence are consistent with an evolutionary interpretation. Gienapp et al. (2007) asked whether migratory birds have been

advancing their spring arrival dates in conjunction with predictions from climate change. An analysis of the results of studies of 249 species produced highly significant correlations between date of arrival and temperature, year, and a major climatic driver, the North Atlantic Oscillation. Although this analysis revealed strong and consistent effect sizes the authors were not able to conclude the extent to which the changes were due to phenotypic plasticity or evolutionary responses, and leaned slightly toward the former.

Experiments provide an important way to resolve the issue of whether responses to anthropogenic selection are due to phenotypic plasticity or evolutionary change. Crispo et al. (2010) asked whether phenotypic plasticity itself has evolved. They summarized results of 20 studies that used common-garden experiments with contrasting conditions to compare rates of change in plasticity in related populations that either had or had not been exposed to anthropogenic disturbance. There were no common trends across taxa, life histories, morphology, or physiology. Interestingly, they found the evolution of both increases and decreases in phenotypic plasticity. There were too few studies to distinguish between different forms of human disturbance, which is an obvious avenue for future research. Until that is pinned down, this meta-analysis is more relevant to evolutionary ecologists than to conservation biologists.

Two studies have examined changes over time in invasive plant species. Hawkes (2007) found that invasive plant species tend to be larger and suffer less herbivory in their new ranges than conspecifics that stayed home. The evidence from this meta-analysis could not distinguish between an evolved response to selection in the introduced ranges, a founder effect or the result of phenotypic plasticity. The study also found an initial escape from herbivory and pathogen attacks, which disappeared after 150–200 years. The author did not speculate on whether this might be due to evolutionary changes in the plants, or in the herbivores and pathogens, adapting to their new hosts. We might expect an arms race to be played out between invasive species and their enemies. Indeed, Doorduyn and Vrieling (2011) summarized data from 15 studies of 9 species of plants reared in common-garden experiments, to test for differences in chemical defense compounds between plants of the same species from invaded and native ranges. They found that individuals from invaded ranges had significantly higher levels of toxic compounds, especially pyrrolizidine alkaloids. These alkaloids help defend against generalist herbivores (which would be expected to be encountered in new ranges) and they can also *attract* specialist herbivores (which would be left behind in the native range). The compounds are thought to be cheap, allowing increased allocation to growth and reproduction. Doorduyn and Vrieling (2011) did not cite Hawkes (2007), so we will go out on a limb here. Putting the results of the two studies together, we have invasive plants evolving cheap toxins (Doorduyn and Vrieling), consistent with the ability to re-allocate resources toward larger size (Hawkes), and perhaps facilitating low initial rates of attack (Hawkes) by generalists (Doorduyn and Vrieling), followed by herbivores catching up over the next 100–150 years (Hawkes). There are lots of leaps of faith in cause-and-effect in our narrative, which will probably be demolished by future meta-analyses.

While we are on the subject of plant invasions, there are other meta-analyses that have tested for differences between invasives and non-invasives in a variety of traits (e.g., van Kleunen et al. 2010), including phenotypic plasticity (Davidson et al. 2011; Palacio-López and Gianoli 2011). While these studies have implications for conservation, they were primarily ecological rather than evolutionary in their outlook, and have therefore not been included in Table 2. Phenotypic plasticity is particularly interesting in an evolutionary

context as it may change over time, in response to changes in both the mean and variance in selection in new environments (Crispo et al. 2010).

The final class of human-caused selection pressures in Table 2 concerns pollution. Two meta-analyses of aerial pollution have assembled a huge number of comparisons of impacts on terrestrial arthropods (Zvereva and Kozlov 2010) and arthropods plus plants and fungi (Kozlov and Zvereva 2011). Our brief review cannot do justice to all of the nuances from the numerous analyses in these papers, which compared performance (mainly body size), abundance, and diversity of organisms in polluted areas with those in less polluted areas. Both studies found evidence that impacts on individual performance declined over time, suggesting adaptation to the effects of pollution. The evidence for this in both studies was based on multiple regressions and while a figure in Kozlov and Zvereva (2011) shows a strong slope of the relationship between performance and time, this figure lacks individual data points. The authors evaluated many factors in addition to the time trend, which we have focused on in this review because of its relevance to evolution, but it would be helpful to use additional methods, such as Akaike Information Criterion (AIC), to test the strength of support for a time trend compared with alternative models. An additional point made by these papers, which is relevant to conservation, is that they found evidence that impacts were exacerbated by climatic factors, which are becoming more important due to climate change.

One major class of human impacts is missing from Table 2, namely evolution caused by exploitation, such as fishing and hunting. We could not find any relevant narrow-sense meta-analyses, as defined at the outset of this review (see also Nakagawa and Santos, 2012), though several studies have shown changes in fish life histories over time that are consistent with potential responses to selection (e.g., Law 2000; Swain et al. 2007; Hard et al. 2008). Studies by Hendry et al. (2008) and Darimont et al. (2009) deserve particular mention, as they did use scale-independent metrics (permitting comparisons among cases), though they did not weight cases by variance or sample size. These studies showed large and rapid phenotypic shifts in a variety of organisms, especially in response to exploitation (Darimont et al. 2009). We cannot yet determine whether these shifts represent phenotypic plasticity or genetic changes, but given the heritability of many of these traits and the strong selection differentials, we can certainly expect an evolutionary component now or in the future.

Local adaptation

Local adaptation occurs when individuals respond to local selection, leading populations to diverge from other populations subjected to different selective pressures. The result of local adaptation is that individuals should have higher fitness in their home environment than in other environments (Kawecki and Ebert 2004). However, many human activities can hamper this process. For example, gene flow increases when individuals from different populations are moved around, either intentionally to rescue vulnerable populations or inadvertently through alien introductions. Local adaptation can also be reduced through changes in habitat quality, and genetic variation may be lost as populations become smaller, reducing the scope for adaptation. Höglund (2009) wrote that 'evidence of adaptation to local environmental conditions is so plentiful it is hard to make a fair review of all the relevant studies'. This statement would suggest that the issue of local adaptation should be ripe for multiple meta-analyses. We found only three such studies with explicit conservation implications: two dealing with fishes and one with plants (Table 2).

These meta-analyses vary in their goals and details, but they all compared fitness-related performance of local or ‘pure’ populations and foreign or ‘hybrid’ populations in both local and foreign environments. Their conclusions are mixed. Leimu and Fischer (2008) and Fraser et al. (2011) both concluded that individuals from local populations of plants and anadromous salmonid fishes, respectively, generally perform better in their home environment than foreigners do, which is consistent with the idea of local adaptation. However, in both cases, foreign populations outperformed local ones in a substantial proportion ($\sim 23\text{--}35\%$) of the comparisons. A remarkably similar result (29%) was found in a purely evolutionary meta-analysis of reciprocal transplant experiments on plants and animals (Hereford 2009). The survival and/or fecundity of individuals in their home environments—two proxies for fitness—were on average 20% (Fraser et al. 2011) to 45% (Hereford 2009) higher than those of foreign individuals in the same environment, while Leimu and Fischer (2008) found a small overall effect size (Hedges’ $d = 0.16$), in favour of local populations.

In contrast to the findings above, McClelland and Naish (2007) found a positive and significant response to outbreeding in a variety of fishes. Outbreeding studies included intraspecific hybridization between ecotypes, between domestic/hatchery and wild populations, and between populations of different locales or years. Hybrid progeny performed better than parental populations in the parental environment, which is not consistent with outbreeding depression, often caused by loss of local adaptation (Allendorf et al. 2001). There was also much variation in explanatory variables, depending on whether the performance of F1 or F2 progeny was measured in the wild or in captivity. However, the authors found evidence of publication bias towards large effect sizes indicative of outbreeding advantage, and most of their results were not robust to the file-drawer problem, whereby non-significant results are not published.

The likelihood of detecting local adaptation might be expected to increase with greater geographic distance between populations if genetic isolation and environmental differences increase with distance. This expectation is not universally supported by meta-analyses. Fraser et al. (2011) showed that local adaptation is stronger as scale increases, but Leimu and Fischer (2008) and Hereford (2009) found a very weak or no association between the relative fitness of local vs foreign populations and the geographic distance between them. In both plants (Leimu and Fischer 2008) and salmonids (Fraser et al. 2011), the magnitude of local adaptation was particularly variable at smaller scales (i.e. $<1,000$ km for plants, <100 km for salmon). This suggests that geographic distance may not tightly reflect actual environmental differences, and a take-home inference of these multiple meta-analyses is that the average magnitude of environmental variation may sometimes be comparable at small and large geographic scales. A fuller understanding of when this is the case will be useful for informing future population restoration efforts.

Concluding remarks

Our initial search turned up more than 1,500 papers that appeared to be meta-analyses related to conservation, and a similar number related to evolutionary ecology. However, when we combined these topics and scrutinized the papers, we were surprised to find only 23 formal meta-analyses linking conservation to evolution. These papers used a variety of scale-independent metrics weighted by variance and/or sample sizes, especially response ratios, differences, and correlation coefficients. Meta-analysts typically had to drop over

half of the papers they wanted to summarize because of lack of basic information such as variances and sample sizes. This is a sad commentary on the standards of reporting in primary research in evolutionary ecology and conservation, although the same criticism has been levelled at pure ecological studies (Gurevitch and Hedges 1999). Most of the meta-analyses provided advice on how such studies can be improved in the future, including pleas for more rigorous reporting of statistics, and it would be interesting to assess whether source studies have been improving in this regard over time.

While most of the studies included moderators in their analyses, they had varying degrees of success in explaining heterogeneity in effect sizes among studies. Sample sizes were often sufficient to break down analyses by broad taxonomic groups, trait categories or study design, but responses to different kinds of human-induced pressures could not be analyzed, which greatly reduces the value of these meta-analyses for conservation management. Unexplained variation often remained, and many of the studies found that the answer depended on either the kind of comparison used in the original study (e.g., common-garden experiments versus comparisons among regions) or the metric used (e.g., measures of genetic variation). These are important conclusions for guiding future research.

Within the intersection of evolution and conservation, most meta-analyses published to date have examined aspects of genetic diversity in relation to fitness traits and population sizes, as well as changes in traits in time and space. This is a narrow range of interlocking subjects, with broad coherence among the conclusions, but it does not reflect the potentially large variety of areas that are relevant to evolutionary conservation. Here are three examples of additional topics that could be tackled using meta-analytical techniques. First, there are numerous studies of dispersal in relation to habitat loss and fragmentation, which could be synthesized to search for general patterns and linked to the genetic analyses reviewed here. Second, there are growing concerns about the impacts of novel pathogens on wildlife populations (MacDonald and Laurenson 2006; Thirgood 2009), which lead to questions about the potential for evolution of resistance to pathogens, including variation due to differences in the ecology and life histories of both hosts and pathogens. Finally, a decade ago Jennions et al. (2001) did a meta-analysis of links between sexual selection and survival. This could easily be tied to conservation to complement studies that search for predictive frameworks of threat-prone species based on behavior and life histories (e.g., Dulvy et al. 2003; Reynolds 2003; Cheung et al. 2005).

We feel we have learned a lot more about evolution from the studies reviewed here than about conservation. Does this mean that studies of evolution and conservation do not have much to contribute to each other, or that people doing meta-analyses have been more interested in evolution than in conservation? A case can be made for both explanations. However, the bottom line is that the current crop of applied evolutionary ecology meta-analyses appears to contribute relatively little to practical conservation. While nearly all of the papers do mention a conservation angle in their introductions or abstracts, most of them have little to say about how conservation biologists and managers can use the information provided. A throwaway comment about something potentially getting worse with climate change is not very useful to people working on the ground, who need not only estimates of the scale of problem at hand (i.e., diagnoses) but also concrete information on alternative courses of action (i.e., prescriptions) and their respective effectiveness.

This apparent disconnect between ‘blue sky’ results and ‘green’ applications is not limited to meta-analyses, but it seems especially acute at the intersection of evolutionary ecology and conservation. The applied evolutionary ecology syntheses carried out to date

have addressed issues with well-developed theoretical underpinnings, whose broad-scale generalities are of interest, particularly to evolutionary biologists who have long been 'happily disengaged from the practical applications of their field to human affairs' (Frankham 1995). In contrast, conservation managers are less interested in generalities (i.e., the overall effect size) than in the specifics (i.e., the effect of moderators on effect size) because the latter can inform the prescriptions that should be considered at a site-specific scale.

If this is an issue specifically with evolutionary biology, we should expect pure applied ecological meta-analyses to be both narrower in scope and more explicit about management implications than the meta-analyses reviewed here. However, we suspect that even applied ecological meta-analyses may fail the practical test, given the existing gap between science and policy (Sutherland et al. 2004; Lawton 2007; Holmes and Clark 2008). Of course, not every meta-analysis needs to make specific recommendations as they can still advance our general understanding of the issues, but we think there is potential for much more focused, management-oriented meta-analyses at the interface of conservation and evolution, which will help to bridge the gap.

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