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RESPONSES TO GLOBAL CLIMATE CHANGE

Phenotypic plasticity and evolutionary demographic responses to climate change: taking theory out to the field

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Summary

1. Rapid climate change both imposes strong selective pressures on natural populations – potentially reducing their growth rate and causing genetic evolution – and affects the physiology and development of individual organisms. Understanding and predicting the fates of populations under global change, including extinctions and geographical range shifts, requires analysing the interplay of these processes, which has long been a grey area in evolutionary biology.

2. We review recent theory on the interaction of phenotypic plasticity, genetic evolution and demography in environments that change in time or space. We then discuss the main limitations of the models and the difficulties in testing theoretical predictions in the wild, notably regarding changes in phenotypic selection, the evolution of (co)variances of reaction norm parameters, and transient dynamics.

3. We use two landmark examples of physiological responses to climate change – trees facing drier climate and extreme temperatures, and marine phytoplankton under rising CO₂ – to highlight relatively neglected questions and indicate the theoretical and empirical challenges that they raise. These examples illustrate notably that age-specific patterns of plasticity and selection on the one hand, and changes in community interactions and functioning on the other hand, need to be further investigated theoretically and empirically for a better understanding of evolutionary demographic responses to climate change in the wild.

Key-words: cline, contemporary evolution, eco-evolutionary dynamics, gene flow, norm of reaction, population persistence, stress tolerance

The creatures which can stand the 'storm and stress' of [...] changes which occur in the environment, by undergoing modification of [...] the structures which they get congenitally – these creatures will live; while those which cannot, will not.

Baldwin (1896)

Introduction

Global climate change occurs at a fast per-generation pace for long-lived large-bodied animals or perennial plants, and also increases variability at shorter time scales, thus

affecting short-lived organisms as well. On the one hand, rapid environmental change affects the demography of species by modifying their geographical range, altering the connectivity of their subpopulations and increasing extinction risk, especially for large organisms with small population sizes. On the other hand, environmental change also can modify the phenotype distributions of populations. Understanding the mechanisms of these responses and their interplay is essential to predict eco-evolutionary dynamics and ecosystem function, and to guide conservation efforts (Ferrière, Dieckmann & Couvet 2004; Saccheri & Hanski 2006; Kinnison & Hairston 2007).

There is abundant evidence that phenotypic change can be rapid in the wild (Kinnison & Hendry 2001; Reznick &

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Box 1. Modelling phenotypic plasticity and its evolution*Types of Plasticity*

A plastic phenotypic trait is described by its norm of reaction, which gives the expected phenotype of a given genotype as a function of its environment of development (or expression). But this seemingly simple definition covers a variety of situations. Some traits are flexible (or 'labile') and respond to the environment throughout lifetime (notably learning and other behavioural traits). Others are 'fixed', and take only one value during lifetime, set by the environment experienced at a critical point during development (mostly morphological traits, such as inducible defences to predators in *Daphnia*). In between are traits that are repeated on discrete occurrences during lifetime, such as yearly breeding dates of birds and mammals, or annual growth rings of trees, which allow measurement of plasticity on individuals instead of genotypes/families (Nussey, Wilson & Brommer 2007). Theory has mostly focused on fixed traits, or rather on traits *that affect fitness only once during lifetime*, because they can be studied in discrete nonoverlapping generations, which are simpler to analyse.

Adaptive or Non-adaptive Plasticity

Most traits respond to the environment to some extent, but these changes need not cause higher fitness across environments (see Grether 2005 for an example of non-adaptive plasticity). Arguably active plasticity, where the environment does not directly provoke the plastic response, but is only used as cue by the organism, is a good indicator that plasticity evolved in response to natural selection. But even more passive plasticity can evolve to become adaptive, if it varies genetically. Non-adaptive (but genetically variable) plasticity of a trait can be due to genetic correlations with other more strongly selected traits, to a change in environmental predictability, or to relaxed selection in low-quality habitats that contribute little to the overall evolution of a species (Holt & Gaines 1992). Plasticity may also be maladaptive in extreme environments, either because selection was never experienced there in the history of the species, or because of a loss of homeostasis (Ghalambor *et al.* 2007).

Models of Plasticity

Phenotypic plasticity can be modelled by treating the parameters of reaction norm shape (e.g. the coefficients of a polynomial) as polygenic traits, and analysing how they respond to selection on the expressed trait (de Jong 1990; Gavrillets & Scheiner 1993a). Alternatively, the values of a plastic trait in different environments are treated as distinct genetically correlated traits (character state approach, Falconer 1952; Via & Lande 1985), which can be extended to continuous environments by means of infinite-dimensional traits (Gomulkiewicz & Kirkpatrick 1992). Despite some controversy (Schlichting & Pigliucci 1993; Via 1993a, b), these models are equivalent (de Jong 1995), and only differ when further assumptions are made about reaction norm shape or genetic variance across environments, so the preferred approach depends on mathematical convenience and the specificities of each system (Via *et al.* 1995). Our argument here is based on the reaction norm approach, because it is a convenient way to model responses to continuous environments like climate variables. The evolution of plasticity (mostly of discrete polyphenisms) also has been studied using optimality models that do not explicitly account for genetic variation in the trait (e.g. Lively 1986; Moran 1992; Sultan & Spencer 2002), but we will not describe them here because they do not allow analysing the dynamics of the evolutionary process.

Phenotypic plasticity is quantified to first order by the reaction norm slope: more plastic genotypes have phenotypes that change faster with the environment. More complex shapes also have been modelled and are expected to evolve under specific conditions (Gavrillets & Scheiner 1993a; de Jong 1999). However, linear reaction norms (i) are the simplest way to include phenotypic plasticity in evolutionary models; (ii) approximate any monotonic reaction norm over a suitable range of environments; (iii) are expected to evolve under symmetrical environmental variation (Gavrillets & Scheiner 1993a); and (iv) are likely to describe reasonably well primary traits that are under selection, but are not direct components of fitness; the latter are expected to have curved reaction norms (tolerance curves) (Lynch & Gabriel 1987; Huey & Kingsolver 1993), causing stabilizing selection on the primary traits (Wright 1935).

Evolutionary Predictions in a Heterogeneous Environment

Via & Lande (1985) were first to use quantitative genetics to model the evolution of phenotypic plasticity in heterogeneous environments. Building on a model by Falconer (1952) for the response of a quantitative trait to selection in different environments, they showed that plasticity should evolve to become 'perfect' (with the optimum phenotype reached in each environment), regardless of whether the contribution of each patch to the next generation depends on the mean fitness of individuals selected there (hard vs. soft selection). This model, however, failed to capture an important aspect of plasticity: that the environment that triggers the plastic response may differ from the one where selection operates on the trait. This occurs when there is a developmental lag for the expression of the phenotype, and/or when plasticity is triggered by an environmental cue that correlates with, but differs from, the actual selective pressure (e.g. a combination of photoperiod and temperature taken as an indicator of future food abundance, Visser 2008). This reduces the predictability of selection, an insight that was introduced in plasticity theory by Moran (1992), and later developed by others in the context of quantitative genetics (Gavrillets & Scheiner 1993a; de Jong 1999; Tufto 2000; Lande 2009). Their main finding was that, in a stationary environment, the degree of plasticity that evolves in the long run does not equal the slope of the optimum vs. environment relationship ('perfect plasticity'). Instead, it is reduced by a factor equal to the predictability of the environment of selection from that of development, defined as a correlation coefficient or regression slope (Gavrillets & Scheiner 1993a; de Jong 1999; Tufto 2000; Lande 2009).

The evolution of plasticity in subdivided populations (with limited dispersal) occupying a spatially heterogeneous environment was addressed by a number of theoretical studies. Models have shown that spatial heterogeneity and dispersal select for higher plasticity (Via & Lande 1985; Sultan & Spencer 2002), but that reduced predictability caused by dispersal between development and selection decreases the equilibrium plasticity (Scheiner 1998; de Jong 1999). Further, the interplay of unpredictable selection and asymmetries in gene flow (and/or variable strength of density dependence) causes genetic differentiation of reaction norms in space (de Jong 1999; Sasaki & de Jong 1999; de Jong 2005). With linear reaction norms, higher plasticity evolves in more extreme environments, if the contribution of variance in plasticity to heritability is larger there (Tufto 2000; Chevin & Lande 2011).

Ghalambor 2001; Uyeda *et al.* 2011) and that it occurs faster in response to human modifications of the environments (including climate change), owing to their unusual magnitude and nature (Palumbi 2001; Hendry, Farrugia & Kinnison 2008; Smith & Bernatchez 2008). Rapid change of adaptive traits affecting fitness is expected to impact the demography of a species, disrupting the separation of ecological and evolutionary times scales (Carroll *et al.* 2007). Although methods that incorporate phenotypic variation in demographic models have been available for some time (Lande 1982; Charlesworth 1994; Easterling, Ellner & Dixon 2000; Van Tienderen 2000; Caswell 2001; Ellner & Rees 2006), it was only demonstrated recently that demographic models do gain explanatory power by including information on phenotypes, implying that rapid phenotypic change significantly affects population growth in the short term (Hairston *et al.* 2005; Pelletier *et al.* 2007, 2012; Ezard, Cote & Pelletier 2009; Ozgul *et al.* 2010, 2012).

Most studied examples of contemporary evolution in response to climate change concern quantitative traits with continuous variation such as body size/shape, breeding time and various aspects of physiology. Such traits generally evolve by polygenic response to selection, even though major genes may be involved at first and accelerate evolution in response to strong selective pressures (Lande 1983; Gomulkiewicz *et al.* 2010). But for most reported cases of phenotypic change in the wild, it is unclear whether they are caused by a change in the genetic composition of the population in response to natural selection (i.e. genetic evolution), or to phenotypic plasticity, the ability of individual genotypes to produce alternative phenotypes in different environments. A recent meta-analysis combining field studies of natural populations and 'common garden' experiments with controlled environments (Hendry, Farrugia & Kinnison 2008) suggested that the faster phenotypic changes observed in human-altered environment are likely to often include a substantial contribution from phenotypic plasticity, a conclusion also reached by Gienapp *et al.* (2008). This has been confirmed empirically in a few wild populations (Charmantier *et al.* 2008; Ozgul *et al.* 2010). It has therefore become clear in recent years that the interplay between evolution and demography in changing environments is at least partly mediated by phenotypic plasticity. This is consistent with the idea that natural selection, which takes place at the population level and with generations as the time unit, is not sufficient for responding to environmental changes that occur at a fast per-generation rate, and in some instances may not actually be necessary for population persistence. However, phenotypic plasticity does not necessarily preclude genetic evolution, and plasticity may itself evolve by natural selection (Scheiner 1993).

Making accurate predictions about the interaction of phenotypic plasticity, genetic evolution and population growth requires integrating theory and data to a degree rarely reached in evolutionary biology, with the notable exception of molecular population genetics. We address

this goal in three steps. First, we review what simple theoretical models of plasticity predict for phenotypic, genetic and demographic response to environmental change. Second, we ask what assumptions of these models may critically limit predictions in the wild and what empirical measurements are needed to assess the validity of these assumptions. And third, we use two case studies to highlight crucial conceptual points that remain relatively neglected by current theory. As this review is mostly about theory and avenues for its application, we do not give an exhaustive account of the relevant empirical literature. Rather, the empirical examples we provide were chosen for their illustrative value, with a focus on physiological responses to global change. A more thorough review of the empirical literature on similar topics can be found elsewhere (e.g. Barrett & Hendry 2012; Vander Wal *et al.* 2012).

Theory on plasticity and demography in novel environments

Baldwin (1896) was first to clearly state within the Darwinian framework that ontogenic, physiological or behavioural mechanisms adjusting the phenotype to the requirements set by the environment can allow individuals and populations to persist under strong stress, and to later adapt by genetic evolution. But the effect of phenotypic plasticity on population persistence in changing environments was not addressed directly until lately, building upon theoretical developments on the evolution of reaction norms (Box 1). The predictions in Box 1 are summarized in Table 1.

CONSTANT PLASTICITY AND DEMOGRAPHY IN CHANGING ENVIRONMENTS

A detailed description of the properties of reaction norms and plasticity is given in Box 1. For simplicity, we focus here on linear reaction norms, but more complex shapes also can be modelled (Gomulkiewicz & Kirkpatrick 1992; Gavrillets & Scheiner 1993) and may be more relevant for some traits. While no reaction norm can be linear indefinitely, this is used here as an approximation that should work relatively well for monotonic reaction norms over a restricted range of environments. We first focus on constant plasticity, such that the slope of reaction norms has no genetic variance, and hence cannot evolve. The influence of constant plasticity on the persistence of a population in a changing environment was investigated in a few recent studies.

Reed *et al.* (2010) studied how phenotypic plasticity (without any genetic evolution) affects population persistence in environments that change randomly in time, with variable levels of predictability. In the context of plasticity theory, predictability is low when the environment that triggers the plastic response is weakly correlated with the one where selection occurs (because of a temporal change in the local environment, or of dispersal between develop-

Table 1. Summary of theoretical predictions on the effect of plasticity and evolution on demography in changing environments, assuming linear reaction norms

	Temporal environmental change	Spatial environmental heterogeneity
Constant plasticity, no evolution	Random fluctuations: high plasticity can cause extinction in unpredictable environments	NA
Constant plasticity + evolution	Sustained change: the critical rate of environmental change for extinction is maximum for a level of plasticity that depends on the cost of plasticity	Plasticity alleviates the negative effect of gene flow on local adaptation and demography. How much it does depends on whether the phenotype is expressed before or after migration
Evolving plasticity	If variance in plasticity increases heritability in novel environments (decanalization), the evolution of plasticity accelerates adaptation, facilitating persistence	Evolving plasticity allows wider geographical ranges and colonization of new habitats, unless the variance load is too large. Higher plasticity in marginal habitats

ment and selection; see Box 1). Reed *et al.* (2010)'s simulations showed that adaptive plasticity (where plastic phenotypic responses to the environment are in the same direction as changes in the optimum trait value) buffers fluctuations of population growth in predictable environments, but amplifies these fluctuations in less predictable environments. The latter decreases the long-run growth rate of a population, thus increasing extinction risk (Lande, Engen & Saether 2003). More precisely it can be shown that, with plasticity but no genetic evolution, the expected load caused by deviations from an optimum phenotype in a fluctuating environment is proportional to $1 + \alpha(\alpha - 2\rho)$, where α is relative plasticity (reaction norm slope scaled to slope of changes in the optimum with the environment, Box 1), and ρ is the correlation between the environment of development and that of selection (or the reliability of a cue that triggers the plastic response). Therefore, even apparently adaptive plasticity ($\alpha > 0$) reduces population growth rate whenever it is larger than twice the predictability of the environment, $\alpha > 2\rho$. In contrast, lower plasticity buffers demographic fluctuations, and when predictability is more than half, any partially adaptive plasticity ($0 < \alpha < 1$) facilitates persistence in a fluctuating environment. Fluctuations of population growth (and the resulting extinction risk) are lowest when plasticity equals environmental predictability (or cue reliability), paralleling previous arguments about the evolution of plasticity (Box 1).

Chevin, Lande & Mace (2010) studied how constant plasticity in interaction with genetic evolution affects population persistence under a sustained trend of environmental change, causing continual directional selection towards an optimum phenotype moving at constant speed. In that case, partially adaptive plasticity reduces the strength of directional selection in every generation, slowing down genetic evolution, but also allows the phenotype to track the optimum more closely (Fig. 1). With linear reaction norms, the second effect more than compensates for the first. Therefore, the maximum rate of environmental change a population can experience without going extinct increases with decreasing difference between the reaction

norm slope and the environmental sensitivity of selection (α closer to 1). But with a cost of plasticity, whereby more plastic genotypes have lower fitness regardless of their expressed phenotype (Van Tienderen 1991; Dewitt, Sih & Wilson 1998; Van Buskirk & Steiner 2009), the maximum rate of environmental change a population can tolerate is highest at intermediate levels of plasticity (Chevin, Lande & Mace 2010). Fluctuations of the optimum around its deterministic trend – as would be caused by, for example, short-term variations in temperature superimposed on a more global warming tendency – have not been included in this model (contrary to an earlier model without plasticity, Lynch & Lande 1993) and would have a complex effect of population growth. Indeed in contrast to the model with no evolution (Reed *et al.* 2010), with genetic evolution, the cumulative effect of plasticity on the responses to selection in all past generations (through its effect on deviations of the mean phenotype from the optimum) would also need to be accounted for.

Constant phenotypic plasticity may also influence local adaptation and population growth in a spatially heterogeneous environment, and the evolution of species' geographical range. Without plasticity, gene flow from neighbouring populations can reduce local adaptation in a heterogeneous environment, affecting local population growth and amplifying asymmetries in deme sizes (Ronce & Kirkpatrick 2001), or restricting a species to a limited geographical range over a continuous environmental gradient (Haldane 1956; Kirkpatrick & Barton 1997). The magnitude of these effects depends on the underlying genetics of selected traits, and in particular, they are less marked when genetic variance is allowed to increase as a result of migration (Barton 2001; Polechova, Barton & Marion 2009; Bridle *et al.* 2010). Crispo (2008) discussed several ways by which plasticity would alter the influence of gene flow on local adaptation. Chevin & Lande (2011) showed that constant plasticity can facilitate invasion of a new habitat by reducing the negative impact of environmental differentiation between the original and new habitats. Colonization is further facilitated if the plastic response is

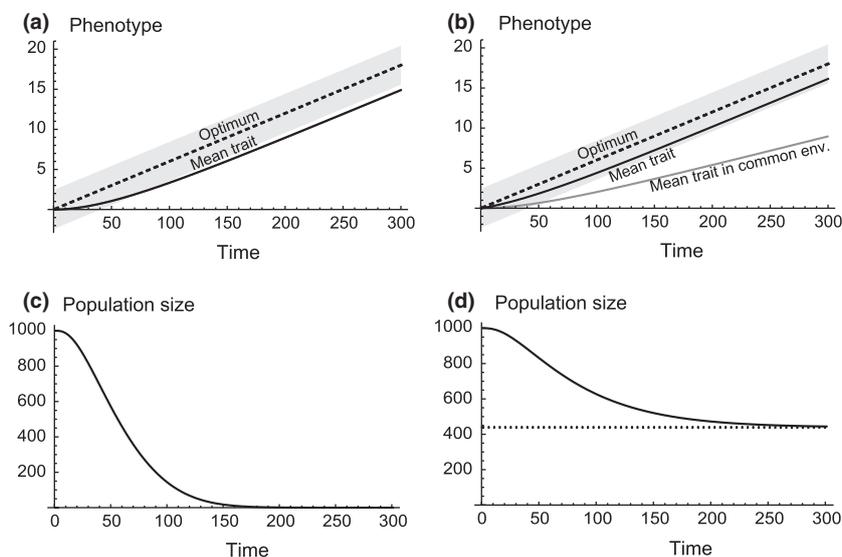


Fig. 1. Evolutionary and demographic dynamics under sustained environmental change. Top: The optimum (dashed line) and mean phenotype (continuous line) are shown for an environment that changes at constant speed. There is no plasticity in (a), while in (b) plasticity is partially adaptive: $b = 0.4B$, with B the slope of changes in the optimum phenotype with the environment (environmental sensitivity of selection). Also shown in light grey shading is the range of phenotypes yielding a positive intrinsic rate of increase. In (b), the dark grey line shows the mean phenotype measured in the original environment, and therefore represents the purely genetic response to selection, removing the contribution from phenotypic plasticity. Although there is less genetic response in the presence of phenotypic plasticity [compare black line in (a) to grey line in (b)], the overall phenotypic change is larger with plasticity [black lines in (a) and (b)], so the equilibrium lag load is smaller in (b). Therefore, a positive intrinsic rate of increase can only be maintained with adaptive plasticity in this example. Bottom: Corresponding population dynamics. Both populations start at the carrying capacity for a population with well-adapted mean phenotype. The population with no plasticity goes to extinction under environmental change (c), while the population with plasticity equilibrates at a positive size [dotted line in (d)] determined by the equilibrium phenotypic lag and the strength and form of density dependence, and thus escapes extinction. The condition for persistence is found when the dotted line in (d) tends towards zero, in which case density dependence can be neglected at equilibrium.

expressed before, rather than after dispersal. Migrants then have lower fitness than residents (offspring of individuals that successfully established in earlier generations), because unlike residents, migrants do not express the correct phenotype in the new habitat, so their contribution to detrimental gene flow is reduced (see also Thibert-Plante & Hendry 2011 for the effect of timing of dispersal in a similar context).

EVOLVING PLASTICITY, RATE OF ADAPTATION AND POPULATION PERSISTENCE

Like any other trait, phenotypic plasticity can evolve if it varies genetically. Despite some interest in the early/mid-twentieth century by Goldschmidt, Schmalhausen, Waddington and others (reviewed in Schlichting & Pigliucci 1998), a proper theory for the evolution of plasticity did not develop until the 1980s. This theory mostly focused on adaptation to stationary heterogeneous environments (Box 1), and the role of the evolution of plasticity for adapting to new environments has received less theoretical attention, even though premises of arguments have been proposed for over a century (Baldwin 1896).

Recently Lande (2009) used Gavrillets and Scheiner's model (1993a, b) to analyse the evolutionary dynamics of linear reaction norms in a new environment, beyond the

usual range of variation. He showed that adaptation to the new environment involves at first an evolutionary increase in phenotypic plasticity (reaction norm slope, Box 1), causing faster phenotypic evolution than with constant or no plasticity. This occurs if variance in plasticity causes the genetic variance of the trait to be higher in the new environment, a pattern that has been repeatedly described empirically, and can be explained by the evolution canalization in the original environment (Holloway, Povey & Sibly 1990; Hoffmann & Merila 1999; le Rouzic & Carlborg 2008; Husby, Visser & Kruuk 2011). Once the optimum phenotype is almost reached in the new environment, plasticity decreases back to a value set by environmental predictability, while reaction norm elevation increases. At the end of this process, the phenotype in all environments is close to the optimum in the new environment, which can be described as genetic assimilation of the initially plastic response (Waddington 1953; Lande 2009).

To address how this process affects population growth and extinction risk in a new environment, Chevin & Lande (2010) used a similar model, but with a cost of plasticity and no environmental fluctuations, and combined it to density-dependent demography. They focused on an abrupt environmental change (or introduction to a new habitat) causing a population to initially decline because of

maladaptation and asked when the evolution of plasticity would allow the population to reach a positive growth rate faster, therefore facilitating population persistence by evolutionary rescue (Gomulkiewicz & Holt 1995). They showed that during the first phase of the process described by Lande (2009), the increase in phenotypic plasticity accelerates adaptation (higher rate of increase in the population mean fitness) by a factor related to the proportion of genetic variance of the plastic trait caused by variance in plasticity. The minimal size reached by the declining population increases exponentially with this parameter, which facilitates persistence, and may even allow overcoming the negative impact of density-dependent competition on population growth. However, because the genetic, and therefore the phenotypic variance, is higher in the new environment, individuals deviate more from the optimum on average, so the equilibrium population size is lower than in the original environment.

The impact of evolving plasticity on population growth in spatially heterogeneous environments, and on colonization of new habitats by dispersers (establishment success and equilibrium population size), was addressed recently by Thibert-Plante & Hendry (2011) and Chevin & Lande (2011). Both found that the evolution of plasticity can facilitate invasion of new habitats, in the presence of gene flow from the original habitat, and that the timing of dispersal relative to development was important for colonization success. A limit is, however, set by the variance load generated in extreme environments by variance in plasticity, with linear reaction norms (Chevin & Lande 2011). For a species continuously distributed over a steep environmental gradient, such as a latitudinal/altitudinal gradient in temperature, the evolution of plasticity increases the response to selection, thus reducing maladaptation induced by gene flow. In interaction with local population growth, this allows a species to occupy a larger geographical range, with higher plasticity in marginal than in central habitats (Chevin & Lande 2011). But to predict range shifts in response to climate change, we would need models for the impact of evolving plasticity on a species' range in environments that vary in space and time. We are not aware of any such model, even though similar ones with no plasticity have been published (Pease, Lande & Bull 1989; Polechova, Barton & Marion 2009; Duputié *et al.* 2012).

Challenges with applications to wild populations

The above theory makes a set of predictions for demographic and evolutionary responses to environmental change, but few empirical studies to date have directly tested or applied these predictions in natural populations. Below, instead of reviewing extensively the empirical evidence for components of the theory, we list some of the main technical challenges with its application, or assumptions that deserve further investigation. We do not address nonlinearity of reaction norms, and the possible disruption

of plastic responses in extreme environments, because it has been the topic of other reviews (Ghalambor *et al.* 2007; references in Box 1); we will describe more mechanistic approaches generating arbitrary reaction norms in the next section.

ENVIRONMENT, FITNESS AND SELECTION

All the predictions above rely on knowledge of the relationship between fitness and measured traits, and most models assume selection for an optimum phenotype. It often makes biological sense that traits involved in adaptation have highest fitness at some intermediate value where, for instance, two opposing selection pressures compensate each other (e.g. intraspecific competition vs. energy budget maintenance for body size). In some cases, an optimum phenotype can be estimated indirectly without measuring fitness, for instance, from a peak of food abundance for the optimal breeding date (Van Asch *et al.* 2007). However, it is often very difficult to measure displacements of (or deviations from) an optimum scaled to the width of the fitness peak, a basic input for many models.

First, some traits are not selected for an optimum. For instance, direct life-history components of fitness are generally selected to increase indefinitely (even though trade-offs may prevent them from increasing jointly, Roff 2002). Such traits often appear to be strongly selected, because they are mechanistically connected to fitness, but most theoretical predictions do not apply to them if they are not selected towards an intermediate optimum. Predictions for the evolution of fitness, and its direct life-history components, should instead include the underlying morphological, physiological or behavioural traits on which they operate selection (Lande 1982; Charlesworth 1994; Van Tienderen 2000); the relationship between these underlying traits and fitness is more likely to involve an optimum phenotype (Box 1).

Even when there is an optimum phenotype, it may be difficult to locate. The most straightforward way is to estimate directional and quadratic selection gradients (average slope and curvature of the fitness landscape, respectively) using a regression method (Lande & Arnold 1983) and then to compute the distance to the optimum by combining these gradients, assuming a given shape of the fitness landscape (usually Gaussian; Kingsolver *et al.* 2001; Estes & Arnold 2007). But this procedure is less accurate if most individuals are on the same side of the optimum, in the considered range of environments. Besides, while attempts have been made to estimate temporal changes in selection (e.g. movements of an optimum) this way (Siepielski, DiBattista & Carlson 2009; Siepielski *et al.* 2011), large uncertainties in estimates of each gradient make it difficult to show that reported variation is not simply caused by errors in the estimation procedure (Morrissey & Hadfield 2012).

Another possible confounding factor is that observed covariances between fitness and traits, often used to pre-

dict genetic response to selection, may actually be caused by nonheritable components of both (Rausher 1992; Morrissey, Kruuk & Wilson 2010), especially as fitness in nature generally has low heritability (Mousseau & Roff 1987). In particular, cryptic micro-environmental variation can bias selection gradients estimated assuming a spatially homogeneous environment. Apparent covariance between fitness and traits can also arise when both are correlated with other traits under selection. While this is easily corrected when multiple traits are measured (Lande & Arnold 1983; Schluter & Nychka 1994; Gimenez, Gregoire & Lenormand 2009), accurate prediction is only possible if most traits affecting fitness – at least those able to evolve or change by plasticity – have been measured. Besides, such correlative measurements of selection do not account for possible hierarchical relationships between traits. Integrated traits (e.g. water use efficiency) result from several underlying traits (photosynthetic rate, transpiration), which themselves also influence other traits under selection (Arntz & Delph 2001). Finer predictions and deeper mechanistic understanding may be reached in that case by deciphering this functional structure, which requires using dedicated methods such as path analysis (Scheiner, Mitchell & Callahan 2000; Tonsor & Scheiner 2007).

Finally, the strength and shape of phenotypic selection can also vary among environments, sexes and life stages (Schluter, Price & Rowe 1991; Coulson & Tuljapurkar 2008). For instance, in the flower plant *Cakile edentula*, Dudley (1996) detected in wet sites an optimum for water use efficiency, and a linear fitness function for leaf size, but selection gradients were quite different in dry sites (note that this result could also be explained by a displacement of a fitness function with unchanged shape). It was also shown that water availability only reduces fitness of plants when it is below a threshold value, but above that threshold causes little or no selection (Ehleringer 1993). Environmental change may even affect which traits are under selection. For instance, for a given nutrient, the challenge may be resource acquisition at low concentrations, but toxicity resistance at high concentrations, which may well imply different traits (Collins 2011b).

GENETIC VARIANCE OF REACTION NORMS

Predicting evolution also requires estimation of genetic (co)variances of traits, which in the wild involves gathering information on relatedness in a pedigree (Kruuk 2004; and Box 2). When multiple traits are measured (which is preferable for better prediction of changes in fitness and demographic parameters), the number of (co)variances to estimate is $n(n - 1)/2$, with n the number of traits, requiring large sample size, and complicating further analysis and interpretation (the same holds for quadratic selection gradients). Although the problem of sample size cannot be avoided, the analysis can be simplified by reducing dimensionality through eigendecomposition (the same

principle as principal component analysis, Blows 2007). Such diagonalized traits may be more difficult to interpret in functional terms (Brodie & McGlothlin 2007). However, it can be argued that principal components based on a combination of genetic variation and selection strength, measuring the phenotypic directions that matter for adaptation (as done by Martin & Lenormand 2006 for mutation effects), are more meaningful in evolutionary terms than the original traits, whose number and measuring methodology are always to some extent arbitrary. Still, using such compound traits to make evolutionary predictions is only valid if environmental changes displace the optimum phenotype without changing the width of fitness peaks.

Box 2. Measuring selection on plasticity in trees

Two main approaches exist to study plasticity and evolution of long-lived organisms. In the first, the contribution of each individual to 'instantaneous' population growth is estimated (e.g. the 'de-lifing' approach of Coulson *et al.* 2006). Because trees are sessile, each individual in a population is easily identified, and progeny can be assigned to parents using genetic markers. Relative fitness can then be estimated as the contribution of each parental tree to the seedling population at a given time and used to estimate selection gradients on traits (Smouse, Meagher & Kobak 1999; Morgan & Conner 2001). Recent developments allow correcting for reduction in fertility with distance between mating pairs; estimating both female (through seeds) and male (through pollen) fitness; and accounting for gene flow from uncensored individuals outside an individual's immediate vicinity (neighbourhood models, Oddou-Muratorio, Klein & Austerlitz 2005; Burczyk *et al.* 2006; Klein, Carpentier & Oddou-Muratorio 2011). While long generation time precludes gathering deep pedigrees, genetic markers can be used to estimate relatedness and genetic variance of quantitative traits (Ritland 1996; Frentiu *et al.* 2008). When local environmental variables are also measured, this can be applied to reaction norm parameters like those described in the theory.

But because this approach does not model explicitly the mechanisms of phenotypic plasticity and selection, it may have limited predictive power (like any correlative method). An alternative is to use mechanistic models where plasticity of integrative traits, their impact on demographic determinants of fitness (growth/competition, dispersal, reproduction, mortality), and the environmental sensitivity of the optimum phenotype, all arise from underlying physiological processes at the individual level. Such biophysical models, stemming from ecophysiology and crop science, have been used to predict population dynamics, community structure, geographical range and evolution for animals (Porter *et al.* 2000; Kearney *et al.* 2009), and are now being developed for trees (S. Oddou-Muratorio & H. Davi unpublished data). Because they allow phenotypic plasticity and selection to emerge from basic physiological principles, and include hierarchical relationships between traits, instead of assuming *ad hoc* shapes for the reaction norm (e.g. linear) and fitness landscape (e.g. Gaussian), such models can facilitate quantification and mechanistic disentangling of the effects of plastic and genetic responses to the environment on population growth. Interpretation may, however, remain challenging because these complex models include numerous physiological processes that are not necessarily easy to relate to macroscopic phenotypes.

Measuring reaction norms and their genetic variation in the wild also requires knowing which environmental variable (or combination thereof) induces the plastic response, and at what point in lifetime (Van de Pol & Cockburn 2011), complicating the procedure relative to controlled laboratory environments for which measurements of plasticity heritability were originally designed (Scheiner & Lyman 1989). Furthermore, even though heritable plasticity has been found in many species (reviewed by Scheiner 1993, 2002), we still know little about how the genetic (co) variances of traits describing reaction norms change in response to selection. Most predictions from quantitative genetic models of plasticity evolution rely on the assumption of constant genetic variances and covariances of reaction norm parameters which, despite being wrong in the long run, approximates well situations where genetic covariances change much more slowly than trait means. Understanding changes in genetic variances of reaction norms is especially important for models where the equilibrium plasticity is reached slowly, such as evolution over an environmental gradient (Chevin & Lande 2011), for which changes in genetic variance can alter the evolutionary outcome in the absence of plasticity (Barton 2001). Theory predicts that under weak mutation, genetic variances in reaction norm elevation and slope (plasticity) at equilibrium both decrease with increasing variability of the environment that triggers the plastic response (but are unaffected by the environment of selection), such that the total genetic variance of the plastic trait equals the ratio of mutation rate to strength of stabilizing selection, regardless of the environment (Gavrilets & Scheiner 1993a; de Jong & Gavrilets 2000). The equilibrium contribution of variance of plasticity to overall genetic variance depends on whether different genes affect different aspects of the reaction norm (e.g. with specific 'plasticity genes'), vs. pleiotropic mutations jointly affecting all reaction norm parameters (de Jong & Gavrilets 2000). Resolving this question requires investigating empirically the underlying genetic and molecular basis of reaction norms (Pigliucci 2001; Beldade, Mateus & Keller 2011).

TRANSIENT DYNAMICS AND STOCHASTIC VARIATION

Finally, although the models above deal with changing environments, analytical results are generally about the long-term asymptotic behaviour (for deterministic change), or the average of a stationary stochastic process (for random fluctuations). However, transient behaviour of the system can also be of interest. For instance, under sustained environmental change (Lynch & Lande 1993; Chevin, Lande & Mace 2010), the time before reaching an equilibrium lag behind the moving optimum is proportional to $1/(\gamma V_G)$, with γ the strength of stabilizing selection and V_G the genetic variance of the trait. This can be substantial when the fitness peak is wide relative to the phenotype distribution (weak selection). This time to equilibrium should be estimated and reported in empirical

studies; if it is much longer than the time over which selection is sustained, then transient dynamics are more meaningful than the equilibrium. In particular, density dependence was neglected in Chevin, Lande & Mace (2010) because it should be negligible close to population extinction, but it may play an important role during the transient dynamics (Fig. 1). Similarly, in a randomly fluctuating environment, the long-term growth rate of a population predicts whether it should go extinct on expectation; but whether each stochastic occurrence of the process (i.e. a given population) goes extinct is also determined by the temporal variance in growth rates (Lande, Engen & Saether 2003).

Emerging conceptual issues raised by case studies

In this final section, we use two emblematic case studies of physiological responses to climate change (for recent reviews on phenology, see Bradshaw & Holzapfel 2008; Visser 2008; Chuine 2010) to highlight conceptual issues that deserve further theoretical attention. These examples, microbial phytoplankton and trees, are not meant to be representative of all studied responses to global change. Rather, they have been chosen because (i) they are at opposite ends of the spectrum in terms of body sizes, life-histories and habitats; and (ii) they illustrate points we believe are biologically important, but rarely investigated theoretically, namely: age-specific plasticity and selection, as observed in long-lived organisms, and the role of plasticity in community responses to climate change.

PLASTICITY AND FITNESS OF LONG-LIVED ORGANISMS: RESPONSE TO DROUGHT AND TEMPERATURE IN TREES

Trees are long-lived sessile organisms capable of long-distance dispersal, forming large populations that often inhabit heterogeneous soil and climate conditions (e.g. altitudinal gradients). They are therefore particularly exposed to temporal and spatial variation in selection, which makes them good models to study variation in plasticity. Furthermore, understanding the relative contributions of phenotypic plasticity and local adaptation to the commonly observed phenotypic clines in trees is key to predicting their potential range shifts under climate change (Aitken *et al.* 2008). Because trees have long generation times, research programmes can only follow populations for a few generations. But for the same reason, the detailed mechanisms of plasticity, and the life-history components of fitness, can be investigated throughout individual lifetimes. In particular, tree species with a seasonal growth cycle offer the opportunity to use dendrochronology to analyse retrospectively plastic responses to annual environmental changes (Fallour-Rubio *et al.* 2009; Martinez-Meier *et al.* 2009).

Most studies on trees are conducted at the population level and *ex situ* (common garden experiments in forest conditions or in growth chambers). In general, these studies find high plasticity, with substantial clinal variation in plasticity across latitudes or altitudes, and possible trade-offs between plasticity and stress tolerance in harsh environments (Matyas & Yeatman 1992; Rehfeldt, Wykoff & Ying 2001; Modrzynski & Eriksson 2002; Corcuera, Gil-Pelegrin & Notivol 2011). Usually, phenotypic plasticity is found to be more genetically variable spatially than temporally (Martinez-Meier *et al.* 2008; Corcuera, Gil-Pelegrin & Notivol 2010), perhaps owing to contrasting levels of environmental predictability in space vs. time. It is thus not currently clear to what extent spatial studies of plasticity in trees will help predict temporal plastic responses and their interaction with demography. Relating plasticity to changes in an optimum phenotype with the environment (environmental sensitivity of selection) is also a challenge. Spatial variation in current population means is sometimes used as a proxy for variation in the optimum phenotype. Using this approach, Rehfeldt, Wykoff & Ying (2001) found that the expected plastic responses in trees can be lower, equal or higher than projected temporal changes of the optimum, depending on the populations.

Only a few studies were conducted at the level of individuals within populations, *in situ*. Fallour-Rubio *et al.* (2009) studied the evolution of ring growth plasticity in *Cedrus* in response to annual summer rainfall, over three generations. They found significant inter-individual variation for plasticity, and significant changes in plasticity across generations, whose intensity varied across different environmental zones in the forest. They found positive inter-individual covariance between plasticity in benign environments and tolerance to stress, contrasting with the trade-offs found at the population level in pines by Rehfeldt, Wykoff & Ying (2001).

The main conceptual challenge for predicting the evolutionary demography of tree populations is understanding how selection operates on plastic traits that affect fitness throughout lifetime, such as annual radial growth or water use efficiency. On the theoretical side, most current work focuses on organisms with discrete generations, whose plastic responses to an environment experienced at one point during their development influences their fitness at a later time point. What would now be needed are models of evolving plasticity that account for (st)age structure, such that the environment can affect phenotypes at multiple ages, and the relationship between the phenotype and fitness components (survival, fecundity) also changes with age, possibly with multiple delays between the expression of a plastic response and selection on the corresponding phenotype. On the empirical side, the challenge is the measurement of fitness and selection for long-lived organisms sampled at multiple ages. Extreme events causing high mortality or reduced

fecundity (such as severe droughts or freezing) are sometimes taken as proxies for selection episodes. However, this is not necessarily valid, because such stresses could affect all phenotypes in the same way, or cause conflicting selective pressures at different age classes that cancel in lifetime reproductive success (LRS), both of which result in no selection. In addition, LRS itself is not a substitute for fitness (Charlesworth 1994; Caswell 2001). In Box 2, we describe two alternative possibilities for empirically studying selection on reaction norms in trees and other long-lived organisms.

EVOLUTION OF COMMUNITY FUNCTION UNDER CLIMATE CHANGE: PHYTOPLANKTON RESPONSES TO CO₂ ELEVATION

Beyond their effect on individual species described earlier, phenotypic plasticity and genetic evolution are also likely to affect the composition and functioning of communities. In the context of global change, a key question is how biogeochemical cycles will be affected, and whether the responses of living organisms will exacerbate or buffer changes in nutrient cycles. In particular, marine microalgae play a key role in global carbon cycling: their primary production is responsible for about half of the carbon fixation on the planet (Falkowski, Barber & Smetacek 1998), and the composition of their communities affects how much food is available for higher trophic levels (i.e. they are the main primary producers). Global extinctions of microbes are unlikely owing to their large population sizes, so the relevant question here is not so much whether evolution and plasticity will facilitate species persistence, but whether and how the overall function of microbial communities will change.

Most empirical studies so far have focused on single phytoplankton species' responses to CO₂ elevation (Box 3), but understanding and predicting ecosystem functioning and nutrient cycling requires studying changes in the overall composition of phytoplankton communities, and in their functional traits. Environmental change can affect (i) community composition (relative abundances of species); (ii) the nature and intensity of species interactions (competition/mutualism) and (iii) community functioning (e.g. rate of carbon uptake). These responses are connected through the ecological traits that mediate adaptation to the physical and biotic environment (Lavergne *et al.* 2010). For example, changes in community composition are caused by differences in population growth rates among species, resulting from adaptation of each of them to its environment (including other species). Species interactions may change as a consequence of plastic or genetic responses to the abiotic environment, for instance when differences in environmental tolerance cause shifts in the temporal overlap of competing species (Gilman *et al.* 2010 describe in length this and other possible mechanisms).

Box 3. Plasticity and evolution of single phytoplankton species in response to CO₂ elevation

Most studies of phytoplankton have focused on key species that dominate blooms and probably are major contributors to the biological carbon sink, such as *Emiliana huxleyi* (Borchard *et al.* 2011). This coccolithophore (the most abundant in the oceans) contributes to CO₂ exchange across the ocean–air interface by photosynthesis and calcium carbonate precipitation. Both processes respond plastically to pH, carbon and other nutrient levels (Engel *et al.* 2005; Lefebvre *et al.* 2012); in particular, the production of particulate inorganic carbon (PIC) is reduced in CO₂-enriched environments, as a consequence of acidification. Müller, Schultz & Riebesell (2010) grew two species of coccolithophore (*E. huxleyi* and *Coccolithus braarudii*) separately under carbon enrichment for tens of generations and found that their plastic responses remained unchanged. However, over very long timescales, microalgae do evolve in response to the changes in nutrient levels (Raven *et al.* 2012). On intermediate (microevolutionary) timescales spanning hundreds of generations, Lohbeck, Riebesell & Reusch (2012) found that the evolved populations calcified more and had higher growth rates than control populations at high carbon. Some lines also calcified more than the control at low CO₂, indicating their reaction norm had a different elevation but similar slope (plasticity) to the control, while in other lines, reaction norm slope (plasticity) differed from the control. This has important implications for the strength of the biological carbon sink in an acidified ocean, as the amount of calcification affects both carbon uptake by phytoplankton and the efficiency of carbon sinking into the deep ocean.

Other studies used model species that are more amenable to large-scale evolution experiments. For instance, the model freshwater alga *Chlamydomonas reinhardtii* was grown for hundreds to thousands of generations under rising CO₂. Microevolution occurred in the same direction as initial plastic responses (for instance, higher photosynthesis rates evolved under higher CO₂), and some initially plastic responses became constitutive under low CO₂ (Collins & Bell 2004; Collins, Sueltemeyer & Bell 2006; Collins 2011a); the latter may be interpreted as genetic assimilation (Lande 2009). Evolved populations became smaller (thus relying more on diffusion for gas exchanges) and lost the ability to induce energy-requiring high-affinity carbon uptake (Collins, Sueltemeyer & Bell 2006). As the latter phenotype was not associated with any measurable adaptive advantage, a possible explanation is a decay of the molecular pathway underlying high-affinity carbon uptake following relaxed selection, after the preferred type of carbon (CO₂ or bicarbonate) became abundant. It remains to be seen whether high-affinity carbon uptake is still lost in more realistic settings allowing for random variation (noise) in carbon abundance over time.

To disentangle the effects of phenotypic plasticity and genetic evolution in such responses, Collins & Gardner (2009) modified the Price equation to partition changes of community functioning traits into components caused by (i) changes in community composition; (ii) average evolution of species in the community and (iii) average physiological/plastic response of those species. More recently, Ellner, Geber & Hairston (2011) proposed a method to partition changes of any ecological variable (e.g. population growth) into contributions from trait change (response to selection, plasticity) and the environment

(including density of conspecifics or interacting species). In the case of marine phytoplankton, carbon enrichment has been shown to change community composition and species succession during blooms in bottle enrichments (Tortell *et al.* 2002) and in situ ocean mesocosms (Riebesell *et al.* 2008). However, these results should be interpreted carefully, as (i) blooms artificially induced by nutrient addition may differ from how nutrient changes will be experienced in terms of timing and intensity and (ii) they show how today's organisms would react in tomorrow's world – that is, they ignore the possible effects of evolutionary change. Collins (2011a) demonstrated empirically that adaptation of *Chlamydomonas* to increasing CO₂ was reduced by the presence of a competitor and that community productivity also decreased relative to cultures of single genotypes. Gravel *et al.* (2011) experimentally modified the relationship between community diversity and productivity in marine bacteria by selecting for generalism or specialism.

We still have little theoretical understanding of how plasticity and evolution should affect community responses to environmental change. Recent theory has shown that competition can slow down evolutionary responses to environmental change (Johansson 2008). More specifically, the rate of genetic evolution in a changing (and spatially heterogeneous) environment was shown by simulations to decrease as the number of species in a community increases (de Mazancourt, Johnson & Barraclough 2008). This is because of an interaction between the evolution and demography, whereby an available niche is more readily filled by an existing species with similar ecology than by the evolution of a more different species. To our knowledge, very little theoretical or empirical work has investigated how plasticity affects species coevolution and demography in a changing abiotic environment (but see Peacor *et al.* 2006; Kovach-Orr & Fussmann 2012).

Conclusions

In the light of the accumulating empirical evidence, it is becoming clear that predicting evolutionary demographic responses to climate change will increasingly rely on studying phenotypic plasticity and natural selection across environments. While theoretical models have started to identify the major processes at stake in the simplest scenarios, further theoretical and statistical developments will be needed to more realistically account for important features of natural populations. We used two examples (trees and microbial phytoplankton) to highlight the most salient questions deserving further investigation, notably selection on plasticity that affects fitness at several points in a lifetime and the role of plasticity and evolution in community composition and functioning in a changing environment.

However, the difficulty in making predictions in the wild is not only methodological, but is also caused by some inherent properties of natural systems (little control on the environment, few replicates, etc.) Therefore, a better understanding and prediction of the interplay of pheno-

typic plasticity, genetic evolution and population growth can only be reached by confronting studies of natural populations to experimental evolution in the laboratory (Chevin *et al.* 2012). This would combine the benefits of replication and control to those of realism, allowing investigation of finer questions about the phenotypic and genetic basis of adaptation and population growth.

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