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Possible Evolutionary Response to Global Change – Evolutionary Rescue?

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1. Introduction

1.1 Climate-induced environmental changes

With a pace that is higher than observed in the past 10,000 years global warming is currently changing the global and local environments. On average, the global temperature has increased by 0.7 degree over the past century and future projections show an acceleration of global temperature rise (Walther et al., 2002) which produces climate-induced environmental changes (CIEC). Increasing the mean temperature furthermore corresponds to an increasing range between the minimum and the maximum temperatures due to a pure scaling effect of the variance with the mean (Pertoldi et al., 2007a). Additional factors may then add even more to the increased range of temperatures combined with increased variability in precipitation patterns. An increased temperature range is translated into a fluctuating selective regime for natural populations and amplified environmental variability ($\sigma^2 e$) which have several consequences at different levels of organization.

In order to understand what limits the ability of species to adapt to CIEC, we need to integrate (local) short-term and (local) long-term changes and to increase our knowledge on the importance of genetic and environmental components on phenotypic variability ($\sigma^2 p$) (Pertoldi et al., 2005). A notorious debate between ecologists and geneticists concerns the relative importance of genetic and ecological factors for the persistence of populations. There is a need for a deeper understanding of how genetic measures can be used to indicate causal processes, including the genetic signature of population declines or expansions due to CIEC. Evolutionary biologists and ecologists have increasingly turned to molecular genetics to study the demographic and genetic consequences of CIEC on populations. However, this approach has some serious limitations: 1) many different population processes lead to similar patterns of genetic structure and 2) population genetic models most commonly applied to these systems are based on the assumption of equilibrium conditions typically not found in nature and surely not in disturbed ecosystems.

1.2 A natural experiment from the past and experimental investigations on the consequences of climate-induced changes

Detailed knowledge on how CIEC have shaped the genetic composition and the present geographic distribution of species can help us to better comprehend the possible future consequences of climatic changes. The biotic effects of Pleistocene glaciations exemplify how climatic changes influence species distributions by alternately inducing southward range

contractions with northward expansions. The geographic patterns resulting from these processes differ with the varying dispersal abilities and ecological requirements of species. The geographical distribution of genetic diversity in species may be used to reconstruct historical biogeographies (Avise, 1998). CIEC do not only affect the distribution of organisms, through changing the abiotic environment, they also change the patterns of biotic interactions between species, and their morphology. More emphasis should therefore be given to morphometrical investigation, which can unravel ecological patterns that are undetectable using neutral molecular markers (Pertoldi et al., 2003). The joint application of different molecular genetic and morphometric methods may prove useful in the description of population structure and help in identifying factors that shape the observed demographical, morphometrical, geographical and genetic structure (Røgilds et al., 2005; Plejdrup et al., 2006).

In particular, studies have been conducted in the attempt to obtain more detailed knowledge on the potential of σ^2p in an evolutionary context. A number of investigations have shown that σ^2p is positively associated with the level of genetic and environmental stresses that individuals experience (Kristensen et al., 2004; Røgilds et al., 2005). Several studies have also tried to elucidate the effect of genetic variability (σ^2g) on σ^2p (e.g. Pertoldi et al., 2003). These studies include analyses of differences in σ^2p between males and females of haplo-diploid taxa, or parthenogenetic and sexually reproducing individuals (Andersen et al., 2002). Pertoldi et al., (2006b) have suggested several methods to split-up the different components of σ^2p (canalization, plasticity and developmental homeostasis), developing algoritms and suggesting the use of clonal organisms to remove the effect of σ^2g and its interaction (GXE) with σ^2e by means of admixture analysis (Pertoldi et al., 2006b).

Several investigations have also been conducted in order to resolve the controversies existing about the causal relationships between molecular genetic variation and phenotype-based measures of success. Pertoldi et al. (2006a) recently suggested that greater clarity would be achieved by partitioning genetic diversity into two components: that arising from adaptive evolution and that resulting from long-term historical isolation. The former can be estimated through analysis of phenotypic variation, while the latter is readily assayed through molecular phylogeography. Both approaches have their place, but measure different components of intraspecific diversity. Pertoldi et al., (2007a) suggested that a proper comparison between genetic variability using neutral molecular markers and genetic variability detected in quantitative and fitness related traits could significantly add to the open debate among evolutionary biologists on the correlation between these two measures. Recent genetics studies are beginning to broaden in scope and impact by attempting to correlate genetic, demographic and phenotypic properties of the same populations (Plejdrup et al., 2006). Furthermore, recent progress in biostatistics and mathematics (e.g. theory of coalescence, Bayesian statistics, individual-based population dynamics, algorithms for efficient simulation and sampling of complex processes), have strengthened our potential to infer population genetic processes of neutral and non-neutral genes via the development of theoretical models (Randi et al., 2003; Pertoldi et al., 2007a).

Modelling techniques having the capacity to incorporate explicit genetic variables linked to important life history traits can also be constructive for the identification of the factors (and their interactions) which are affected by CIEC and can be used as complementary tools (Strand, 2002; Bach et al., 2007). Simulation models can also easily accommodate different global change scenarios, which may not be readily accomplished by mathematical analysis.

Stochastic genetic models may mimic events at individual loci, so-called finite loci or allelic models, or may be parameter based, unfolding the average genetic effects according to quantitative genetics theory (Verrier et al., 1990; Wang, 1996).

1.3 Consequences of CIEC on biodiversity

Determining the biodiversity impacts of climate change is a great challenge (Schwenk et al., 2009). The major consequences of CIEC for biodiversity at various scales include: distributional range of species, phenology, community structure and species interactions (Walther et al. 2002). The demographic context of $\sigma^2 p$ has considerable significance to the process of adaptation. Not only does dispersal among patches influence the evolution of traits and their plasticity, but the changing meta-community also plays a role in determining how populations respond to change (Angilletta, 2009; Mitchell & Angilletta, 2009). Given this situation, predictions at the community level seem either pointless at present or unworthy of pursuit (Ricklefs, 2008), especially since initial conditions, instabilities, and model errors should greatly affect the impact of climate change on ecological communities. Substantial shifts in the ranges and phenologies of species from an array of groups have occurred in response to climate change (Steltzer & Post, 2009). This emphasises the importance of mitigating such shifts through e.g. corridors or by securing large coherent areas with suitable habitats for wildlife. Without such initiatives many populations may become extinct due to combined effects of environmental stress, lack of evolutionary potential and inbreeding depression.

1.4 Shifts in the ranges and phenologies of the species as a consequence of climate-induced changes

Biologists no longer doubt that biological systems have already responded to the current global anthropogenic changes in climate. Many studies have demonstrated substantial shifts in the ranges and phenologies of species from a broad array of taxa, indicating a coherent fingerprint of climate change (e.g. Chen et al., 2009; Steltzer & Post, 2009; Knudsen et al., 2011). Given the substantial evidence of shifting ranges and phenologies, and of substantial range shifts in the past (Davis & Shaw, 2001), much attention has also been given to forecasting the likely effects of ongoing climate change on species distributions and ecosystems from these perspectives (e.g. Kearney et al., 2008). A large, and often contentious, literature has developed about how changes in species' ranges should be modelled and how biotic interactions mechanisms might be incorporated to generate novel insights (e.g. Jeschke & Strayer 2008; Keith et al., 2008).

2. Exploiting population variation and molecular techniques

Although environmental variation is not necessarily reflected in transformed vital rates, such as growth rate, interplay between environmental variation and population dynamics has been shown in a variety of species Stenseth et al., 2002). Understanding the consequences of demographic stochasticity in populations requires information of local fluctuations in population size, extinction probability and colonisation potential as well as reproductive success, which can be gained from population dynamics analyses. DNA analyses are progressively used to estimate the extent and organization of genetic diversity in populations in order to infer the causes of spatio-temporal dynamics (Schwartz et al.,

2007). Such assessment is performed by investigating the degree of neutral genetic variation, which is informative in inferring ancient or recent historical dynamics of populations. Information on the genetic composition of a populations prior to environmental perturbation is now accessible thanks to the recent progress in biostatistics and mathematics (e.g. theory of coalescence, Bayesian statistics, individual-based population dynamics, algorithms for efficient simulation and sampling of complex processes), which have greatly improved the possibility to infer population genetic processes through the development of theoretical models (Stephens & Balding, 2009). Going beyond plain parameter estimation is possible in applying a Bayesian approach, which can integrate both genetic and non-genetic data and hence test hypotheses about the factors that control demographic and genetic changes. In particular, the development of Bayesian models aimed to infer historical population dynamics and population parameters are particularly promising (Riebler et al., 2008).

The causal relationship between molecular genetic variation and phenotype-based measures of success are associated with some debate. Part of this incongruity stems from confusing the levels of organization at which genetic variation and phenotypic accomplishment have been conceptualized (Coulson et al., 2006). Further, molecular markers cannot identify the likelihood of loss of genetic variance in traits of ecological significance, as the correlation between molecular diversity (which is per definition neutral) and ecologically relevant traits (which are per definition non-neutral) is weak and becomes even weaker in expanding or declining populations. However, the attempt to correlate neutral and non-neutral variability can be made by using a promising new tool in conservation genetics consisting of the single nucleotide polymorphisms (SNPs). It is at present viewed as the richest polymorphic genetic marker in many genomes and may get round some of the problems related to microsatellites because of the enhanced resolution of genetic variation. In natural populations SNPs hold the potential to expand our ability to survey both neutral (non-coding region) variation as well as genes under selection (coding region), while also providing wider genome coverage compared to microsatellites (Morin et al., 2004). Further, moving the genomic methodology from lab-model organisms to non-model organisms is now becoming achievable, allowing genomic analysis in a population- and species wide fashion (Mitchell-Olds et al., 2008). Until recently, the genomic tools and resources have unfortunately been limited when it came to key ecological species as opposed to models species with plenty of genomic approaches readily available.

Recent identification of functional genes and genes linked to quantitative traits are opening the way to the analysis of functional genes and components of genetic control of physiological processes and are therefore expected to contribute to the understanding of local adaptation (Marsano et al., 2010). Population genomics will very soon add important contributions to these issues, delivering substantial amounts of data on regulatory polymorphisms on a genomic scale. Moreover, we may address the question of whether the regulatory variation per se cause adaptation to local conditions and whether it is able to significantly alter life-time reproductive success.

Quantitative genetic analyses are important in the assessment of the extinction risk since this approach can give information on the amount of non-neutral genetic variability present for a given trait. This information enables us to scrutinize fitness components on various genetic and environmental backgrounds, producing information on the fate of genetic diversity and the force of selection acting on the populations. Note however, that in practice we are thus limited to manageable organisms with short generation times. Nevertheless our ultimate

aim is to determine how much a response of a given trait to environmental change is due to plastic and/or evolutionary response. Such information is becoming very relevant for evolutionary biology as there is a need for detailed studies on how variation at the level of genes translates, through developmental and physiological processes, into phenotypic variation for ecologically significant traits (Coulson et al., 2006).

Quantitative genetic investigations have thus far often been limited to laboratory conditions and the neutral molecular markers in natural populations are not necessarily relevant to understand the evolution of functional genes subject to selection, which point to the potential adaptability of a population to environmental changes. In natural populations it is difficult to show selection (let alone to quantify). However, genome scans and association studies are increasingly promising due to new statistical methods with improved power (Stephens et al., 2009). Although identifying selected and functionally important genes is no easy task, genome scans offer the possibility of finding genomic domains with selective value, which in turn is a first step in separating selection from the background of random genetic drift. This would make way for describing how changing environments (and fragmentation) can affect different domains of the genome. Hence, finding genomic domains under selection may be at least as useful as gene finding per se. A combination of ecological genomics and quantitative genetics will therefore lead to a greatly increased understanding of ecological responses, starting from genetic variation in natural populations to the description of shifts in phenotypes as a result of evolutionary responses to environmental changes (Luikart et al., 2003).

3. Theoretical approaches

The development of theoretical models and the use of computer simulations have also contributed significantly to the understanding of the consequences of CIEC. These models include stochastic environmental effects, allowing us to make probabilistic predictions that can be reasonably precise when we consider averages over large scales. Considerable progress has been achieved in incorporating age- or stage-structure into population genetic models, mostly in the context of life history evolution and estimation of the effective population size (N_E) of large and stable populations (Engen et al., 2010). However, knowledge on the interaction between age- or stage-structure and other factors, such as variance in reproductive success, temporal fluctuations in population size, is still fairly limited. Although attempts have been made to combine ecological and genetics theory, there is still insight to be gained from integrating the disciplines further.

Deterministic simulations are based on algebraic equations that predict the likely outcome of sampling, while stochastic (Monte Carlo) simulation models mimic random processes. Although being transparent and analytically tractable, deterministic predictions cannot deal with the same level of complexity over many generations as stochastic simulations. The benefit of combining these approaches is evident from simulations used to verify the accuracy when prediction equations are developed. Stochastic simulations are relevant for the design of risk estimates and there are no inherent limitations excluding representation of the genetic level.

The study objects, such as populations or individuals, do not necessarily comply with the mean field assumptions that all units are organised as uniform masses and interactions are unconditioned and can be averaged. In such cases the individual-based models (IBM) or agent-based approaches can be appropriate ways to allow variation in many aspects of the

individual's characteristics as well as variable and conditional interactions (Travis et al., 2009). Likewise the geospatial implementations of IBM can account for specific spatial effects. This approach can be especially relevant for heterogeneous populations of higher animals in spatiotemporally heterogeneous environments with behaviour depending on its own state, the state of conspecifics, or the specific states of the environment (Bach et al., 2006; Bach et al. 2007). In other words the individual in an IBM does not perceive and interact with 'the average individual' of an abstract averaged population according to an average encounter rate and it does not experience the average environment. However, as entities, interactions and environment can be freely defined it follows that the extreme flexibility can become a challenge when designing simulations to address simple questions. In terms of genetics, another advantage of IBM is the straightforward implementation of genotypes, representing either neutral or selected genes where the latter permit the agents to adapt to changing environments. Such models are often referred to as complex adaptive systems (CAS) (DeAngelis & Mooij, 2005). Also the fact that events in IBM simulations are inherently stochastic may prove an advantage when the goal is to obtain probabilities. Much depends on the specific question and available data.

4. Developments in geographical ecology for understanding the consequences of climate-induced environmental changes and its interactions with other biotic and abiotic factors

Given that human impacts in terms of both anthropogenic climate warming, habitat loss and fragmentation, are likely to increase over the 21st century (Smith et al., 2009), the consideration of geographical ecology research is an important new avenue of research.

Therefore, the inclusion of new developments in geographical ecology towards much improved quantification of the determinants of species distributions and diversity patterns will be interesting (Guisan & Zimmermann, 2000). Notably the role of geographic variation in environmental factors such as climate creates an important basis for predicting responses to future climate change (e.g. Thomas et al., 2004). Furthermore, climatically-driven global geographical variation in metabolic rates may both be of fundamental importance to biodiversity and ecosystems and a determining factor in organism sensitivity to stressors (Dillon et al., 2010). Another motivation to look towards geographical ecology is the question of ascertaining effects of habitat destruction and fragmentation on species distribution changes from the separate effects of stressors, as well as their interactions (as fragmentation may affect exposure and susceptibility to environmental stressors (Gandhi et al., 2011).

5. Demographic and genetic consequences of CIEC

Environmental factors and their changes are to a large extent mirrored in the genetic composition of affected populations, which in turn impact the potential for adaptation to future selective forces such as CIEC. Even small alterations of environmental conditions can affect the genetic composition of populations, both via demographic and selective responses (Lande & Shannon, 1996; Björklund et al., 2009). Adaptation is one of the core principles in evolutionary biology and natural selection is universally regarded as the primary cause of evolutionary changes (Vermeij, 1996). The effects of rapid environmental changes, such as global warming, can cause problems particularly for small, isolated populations. Small

populations may lack the genetic diversity that would allow adaptation to a new environment, and thus might risk extinction (Spielman et al., 2004). Further, genetic drift in small populations (Gilpin and Soulè, 1986) leads to loss of genetic diversity, further depressing the evolutionary potential and thereby the ability to respond to changing environments (see Lynch 1996). Additionally, in small populations the chance of mating among relatives is increased due to the limited number of individuals, which causes inbreeding and further decreases mean fitness (Spielman et al., 2004). The increased probability of mating among relatives and the accelerated rate of loss of genetic variability in populations are strongly associated with a reduction of NE which is the size of an "ideal" (stable, random mating) population that results in the same degree of genetic drift as observed in the actual population (Wright, 1931). Due to the numerous ways in which natural populations can deviate from the "ideal" population, N_E may be only a fraction of the population census size (N) size (Lande and Barrowclough, 1987). The N_E of a population can predict its capacity to survive in a changing environment more reliably than the census size and/or the amount of genetic variability (Nunney, 2000).

Global scale environmental change may affect the local N_E in several ways that may not be entirely independent. Firstly, as environmental changes accelerate, the demand for rapid adaptation becomes more pronounced, as in the simplest case where an optimum mean trait value shifts as a result of e.g. a rise in mean temperature. This requires a certain 'standing crop' of genetic variation in order for the population to track the moving optimum. Failing to do so, the populations may suffer demographically from the load of being maladapted. Secondly, the variance of environmental conditions may increase putting its toll on genetic variance by lowering the harmonic mean (HM) through the population dynamic response to environmental fluctuations. Theoretical models predict that fluctuation in population size is one of the dominant causes of reduction of N_E and the low N_E/N ratios (Kalinowski and Waples, 2002). If generations are non-overlapping, N_E can be approximated as the HM of the population census size N (Caballero, 1994).

The expected heterozygosity (H_e), a measure of genetic variability, can provide an indication of the immediate evolutionary potential of a population, but it has no necessary relationship to longer term potential (Nunney, 2000). This is particularly true when the environment of the population is changing. The notion of N_E can therefore be viewed as a bridging point between ecology and genetics, with the ecological characteristics including life history traits, social structure and population dynamics determining N_E and hence the rate of loss of genetic variation (Caballero, 1994). Likewise, environmental factors and changes thereof are mirrored in the genetic composition of affected populations. Moreover, recent work points to the impact of altered environmental variability on the variation of vital rates, which in turn obviously affects the demography and therefore N_E (see Boyce et al., 2006 and references therein). The effective population size is therefore related to the temporal variability of the population, which is a fundamental property of the ecological system. Theoretical studies have established that both statistical and biological mechanisms have the potential to influence the temporal variability of populations (Tilman, 1999). Statistical averaging and mean variance rescaling are predominantly statistical mechanisms, while species interactions and contrasting responses of different species to environmental fluctuations are primarily biological mechanisms. These mechanisms may very well be interdependent, and some have both statistical and biological elements (Tilman, 1999).

Most ecologists are familiar with the general propensity of the variance (δ^2) to increase with the mean (μ) which is why ecological data are often log-transformed prior to statistical analysis. For populations experiencing constant per capita environmental variability, the regression of log δ^2 versus log μ gives a line with a slope of 2 and this positive relationship between δ^2 and μ can be described in terms of Taylor's power relation (Taylor, 1961),

$$\delta^2 = K\bar{\mu}^{\beta} \tag{1}$$

where, K is a constant, and β is the scaling coefficient, which here is equal to 2. Larger values of β indicate that the variance increases more rapidly with μ than expected. Values of $\beta > 2$ are not uncommon, and several authors have suggested that β may lie anywhere in the range of 0.6 to 2.8 (Taylor and Woiwod, 1982). Taylor and Woiwod (1980) estimated β for 97 aphid species and for 31 of these species β was found to be above 2.

Several authors showed that environmental stochasticity (σ^2_e) can lead to a substantial extinction risk also for large populations, not merely small ones, and especially so if the population growth rate is low (Lande, 1993; Foley, 1994).

Mean time to extinction is a function of the carrying capacity (K_c) raised to the power of $(K_c)^\omega$ where

$$\omega = \frac{2r}{\sigma^2_e} - 1,$$

and where σ^2_e is the environmental variance due to environmental stochasticity, which is the most instantaneous effect on the risk of extinction; and r is the mean growth rate of the population, which is affecting the long-term persistence of populations, (Saltz et al., 2005). There is at the present a general accord that in a stable environment the mean time to extinction of a local population grows with the carrying capacity K (Lande, 1993) whereas under adequately strong, uncorrelated environmental stochasticity, the dependence is characterised by a power law (Foley 1994). Hence, large populations should practically never go extinct for the duration of ecological timescales. The main reason for the discrepancy between this prediction and reality is that real populations are also exposed to deleterious processes other than demographic stochasticity (σ^2_d) which with small population size, is playing a large role on the probability of extinction. Although the time to extinction is expected to increase with population size, other factors influence the dynamics of populations as e.g. mechanisms of density dependence and population growth rates (Sæther & Engen, 2003). Fluctuations in population size is a factor that strongly affects the extinction risk of a population, because larger fluctuations increase the probability that one of these excursions in population size reaches zero with extinction as a result (Boyce et al., 2006; Pertoldi et al., 2008).

Intuitively, for a given average abundance, one expects the risk of extinction to increase with temporal variability; however, many studies conducted on long-term data from natural populations have found a contradictory result (Pimm, 1993). These studies use temporal variability as a direct proxy for population vulnerability, where population variability measures are calculated from time series data as standard deviations (sd), log$N$ or coefficient of variation (CV). The reasons for the discordant results obtained in these correlational studies have been the subject of a debate and the relative importance of density dependence process on population dynamics has been compared to the relative importance of environmental variability (Turchin, 1998), which is probably, the most important of

stochasticity affecting population viability (Drake & Lodge, 2003). An additional complication consists of considering the effect of the colour of the environmental noises (i.e. temporal environmental autocorrelation which can be negative, positive or uncorrelated) (Ranta et al., 2008; Björklund, 2010). Theoretical studies, however, have produced conflicting results even when predicting the sign of the effect of the different kind of noises (Halley & Inchausti, 2002), depending on interactions between the environmental noise and demographic processes (Ruokolainen et al., 2009) and on the time scale at which the amplitude of environmental noise is measured (Heino et al., 2000).

Extinction risk can also be deeply influenced by the community context (Guichard, 2005) and/or spatial structure (Engen et al., 2002). Currently, it is possible to simulate the realistic and complex population dynamics and hence quantify extinction risks (Schodelbauerova et al., 2010), and the predicted extinction risk can be a more objective measure rather than many other metrics (Fujiwara, 2007). Modelling approaches for quantifying extinction, such as population viability analyses, are however often faced with so many levels of uncertainty that their utility has been questioned by some researchers (Fieberg & Ellner, 2000). Additionally, before the analyses of the more complex models, it would be natural to understand the fate of a single local population in absence of the various possible biotic interactions (Hakoyama & Iwasa, 2005).

There is a general consensus among ecologists that assuming an initial population size which is large enough for the population to avoid a rapid initial extinction, the distribution of extinction times is exponential in almost any kind of population model, including very complex individual-based models (Grimm & Wissel, 2004). Thus, in this case, the mean time to extinction is a sufficient proxy for predicting the full distribution of extinction times. As previously mentioned, population fluctuations also act to reduce HM of the population census size estimated over time (Pertoldi et al., 2007b). Pertoldi et al., (2007b, 2008) proposed a simple model to estimate the risk of extinction and population persistence based on a description of the HM, defined by the two parameters of the scaling equation (Pertoldi et al., 2007b). The risk of intercepting zero is highly dependent on the way the variance of the population size relates to its mean and Pertoldi et al., (2007b) demonstrated that the minimum population size required for a population not to go extinct can be determined by a scaling equation relating the variance to the arithmetic mean. Pertoldi et al., (2007b) showed that for values of β >2 the relation between μ and HM remains non-linear and non-monotonic as with increasing HM first increase, followed by a domain of decreasing HM with increasing. Therefore, it can be deduced from the model that for certain values of K and β a population will become extinct even if its population size is sufficiently large to restrict the impact of σ^2_d. This description allows a separation of the domains of population persistence versus those of extinction and hence allows the identification of populations on the verge of extinction. The method also presents the estimated minimum population size required for population persistence in the presence of different levels of σ^2_e. To sum up, the model shows that maximizing the population size may not always reduce the extinction risk. Additionally, increasing population size is not always equivalent to an increasing N_E, but may decrease and hence lower the adaptive potential critical to the evolutionary response to changing environments.

At the same time some factors can increase β above 2 and therefore it would be interesting in relation to the application of the following model described below: Pertoldi et al., (2007b; 2008) has shown that environmental stochasticity either increase or reduce the amplitude of

the population fluctuations depending on the sign of the correlation between population size and environmental fluctuations as:

$$\sigma^2_{tot} = \sigma^2 + \sigma^2_e + 2rp(\sigma\sigma_e) \,, \tag{2}$$

where σ^2_{tot} is the variance of the population size in the presence of environmental noise, σ^2 is the variance of the population size in absence of environmental noise, σ^2_e is the environmental noise and $r(\sigma\sigma_e)$ is the covariance between the environmental noise and the population fluctuation. The covariance is given by two times the product of rp and the sd of the population size and the environmental fluctuations (σ and σ_e respectively). Hence, a negative correlation (rp < 0) between environmental stochasticity and population fluctuations will decrease the fluctuations of the population size, with $\sigma^2 tot < \sigma^2$, whereas in case of a positive correlation (rp > 0) we will observe an increase in population fluctuations in the presence of environmental stochasticity ($\sigma^2_{tot} > \sigma^2$). Clearly if σ^2_e overwhelm σ^2 of the population dynamics, it will be the main determinant of the amplitude of oscillation of σ^2_{tot} whatever the correlation between σ^2_e and σ^2 is.

Hence, a population near the carrying capacity with β near the value of 2 should be more prone to extinction, as when an environmental stochastic event is added β will become larger than 2, which means an increased risk of extinction. The fact that β depends on the density of the population, makes it quite evident that β and K should be considered when interpreting the fluctuations of a population. As demonstrated by Pertoldi et al., (2007b), extinction risk of populations can only increase with increasing population size only if the β values can reach values above 2 (β > 2). Pertoldi et al., (2007b) showed that for certain combinations of β and K (β >2 and $K < \mu^{(2-\beta)}$, the following equation:

$$\overline{\mu} - \sqrt{K\overline{\mu}^{\beta}} = 0 \tag{3}$$

predicts the largest mean population size allowed before extinction is expected. Furthermore, Pertoldi et al., (2008) obtained after several rearrangements, the following inequality:

$$K^{\frac{1}{(2-\beta)}} < \overline{\mu} \tag{4}$$

Where μ represents the minimum viable population size necessary for the population to persist. Values of β > 2 are not uncommon, and several authors have suggested that β may lie anywhere in the range of 0.6 to 2.8 (Taylor and Woiwod, 1982). Factors increasing β above 2 could therefore be interesting in relation to the model. Some possible scenarios where it can be speculated that β values could reach values above 2 could be for example when two species interact in a predator-prey interaction, or there is a primary consumer of a resource which fluctuates with time.

Another factor potentially affecting the σ^2 is temperature fluctuations and there is currently general concurrence that global warming is affecting animal and plant populations in multiple ways (Parmesan, 2006). Different degrees of σ^2_e and their correlation with the dynamic of the fluctuations of the population can allow the population to reach values of β above 2 and change the K values. Note also that the risk of β values above 2 is increasing when the population is approaching its carrying capacity.

Given that HM is mainly dominated by the minimum value reached in a fluctuating population, it must be kept in mind that even if the environmental stochasticity does not have a constant period of fluctuation (and is not synchronised with the population fluctuations), what will be important for the determination of HM is the maximum positive value of rp and/or the minimum peak of the environmental stochasticity fluctuation reached in a given time interval. More precisely it will be the maximum rp observed when the population size values are below and when the first derivative is negative ($f^i < 0$). In this interval the population will attain its smallest value, which in turn strongly influences the HM. Without evoking the correlations between environmental noise and population fluctuations it seems rather intuitive that if the noise is positively autocorrelated (reddened), especially in the time interval where the population size is below the average of the fluctuations and f^i is negative ($f^i < 0$), the probability to attain the minimum value of the population size and consequently the minimum HM is increased and this phenomenon should be taken into account due to evidence that long-term ecological data sets demonstrate reddened spectra (Halley & Inchausti, 2002).

Temporal variability estimated using sd, logN or CV as a direct proxy for population vulnerability, could be misleading as such measures of variability only should be used if the variance scales proportionally to the square of the mean ($\beta = 2$), and we have illustrated how β often differs from 2. Consequentially, there is a call for for detecting regime shifts in the dynamic behaviour of populations as changes in the global environment begin to accelerate and it would be interesting to establish a method which allows an estimation of the importance of σ^2_e on the two parameters β and K and on how much alteration of the parameters will push the population towards the extinction threshold. There are, however several other complications associated with the preservation of biodiversity and/or genetic variability: An enduring debate in ecology has also been how the diversity affects the temporal stability of biological systems. The ecological consequences of biodiversity loss have gained growing attention over the past decade (Bangert et al., 2005; Reusch et al., 2005). Current theory suggests that diversity has divergent effects on the temporal stability of populations and communities (Tilman, 1996). Theoretical work suggests a paradoxical effect of diversity on the temporal stability of ecological systems: increasing diversity should result in decreased stability of populations, while the community stability enhances (Tilman, 1996). While empirical work corroborates that community stability tends to increase with diversity, investigations of the effect of diversity on populations have not exposed any clear patterns. This consideration, together with the observation that changes in vital rate may have opposing effects on growth rate and N_E, is of key importance, as it can produce disagreement about the optimal management strategies.

It is well known that demographic instability in a population is translated into fluctuations of N and a reduced N_E which is close to HM of the varying N values (Vucetich et al., 1997). Therefore, a management strategy with the goal of preserving biodiversity on the community level could theoretically lead to a reduction of N_E in single populations. In the same way, the attempt of increasing growth rate in a population by modifying some of the vital rates can also produce a reduction of N_E. An increase in growth rate will increase N and therefore reduce the demographic stochasticity which is related to the population's risk of extinction, but may simultaneously lead to a reduction of the genetic diversity.

Another question emerges from considering both short- and long-term adaptability in a changing environment and whether genetic variability is always beneficial. This is not

always the case as for example in constant environments genetic variability in a quantitative character creates a segregational load each generation due to stabilizing selection against individuals that deviate from the optimum phenotype (Lande & Shannon, 1996). Consider a presumably ordinary situation where natural selection acting on quantitative characters favours intermediate phenotypes. In an intermediate-optimum model, the genetic variability may be either beneficial or detrimental, depending on the pattern of environmental change (the frequency, the amplitude and the degree of autocorrelation of the environmental oscillations) (Lande & Shannon, 1996, Björklund et al., 2011).

The genetic consequences of CIEC can be subdivided in two main categories, namely consequences in small populations and consequences in large populations:

In small populations, random genetic processes (genetic drift) lead to loss of genetic variability, which may depress the evolutionary potential and thus the ability to respond to changing environments (Pertoldi et al., 2006a). It is also anticipated that populations only persist if the rate of adaptive evolution at least matches the rate of environmental change since the evolutionary response of quantitative traits to selection necessitates the presence of genetic variability (Burger and Lynch, 1995). In fact, this is the case even in the presence significant capacity to respond plastically, including adaptations in behaviour, physiology, morphology, growth, life history and demography. The rate of loss of genetic variability in populations is associated to a reduction of N_E. Reduction of N_E due to amplified population fluctuations, reduce the evolutionary potential, by reducing the additive genetic variance (σ^2_a) and the heritability (h^2) of the traits, which in turn is inversely related to σ^2_e.

In large populations, the regime of alternating selective pressures has the potential to increase the average population fitness, selecting for genes implicated in the expression of plasticity. Various modelling approaches have shown that to optimize fitness, phenotypic plasticity evolves by trading the adaptation to acquire resources against the costs of maintaining the potential for plasticity (Ernande & Dieckman, 2004). Plastic responses include changes in behavior, physiology, morphology, growth, life history and demography, and can be expressed either within the lifespan of an individual or across generations (Pertoldi et al., 2005; Røgilds et al., 2005). Two ways of adapting to environmental changes are therefore possible, by evolutionary or by plastic responses, including maternal transmission (trans-generational plasticity). Hence, the survival of populations relies on genetic variation and/or phenotypic plasticity. Populations with small N_E and/or little genetic variability have mainly the option of adapting in a plastic way, therefore the importance of plasticity is quite evident (Pertoldi et al., 2007b).

6. Conclusions

6.1 Future directions

In conclusion, to test the robustness of the theoretical foundations of evolutionary and ecological genetics, three main categories of questions should be answered, using a multidisciplinary approach consisting of: (A) experimental population genetics, (B) collection and analysis of empirical data, and (C) computational population genetics combined with ecological information as for example life history characteristics of the study organism.

6.1.1 Experimental population genetics

Numerous experiments should be conducted including different model organisms. Many of these experiments should be based on innovative methods accounting for the experimental

errors due to unpredictable environmental components (for applications see Kristensen et al., 2004). Clonally reproducing strains should be used to study the extent of adaptive phenotypic plasticity, and maternal effects, including the effect of parental ageing. The use of clonal strains will allow us to exclude the genetic components and their interactions with the environment. Therefore, unbiased estimates of genetic and environmental canalization, plasticity, developmental homeostasis and σ^2_e, will be obtained. A more correct interpretation of the interplay between these parameters will provide important contributions to: 1) The evolutionary importance of phenotypic plasticity, maternal effects, environmental and genetic stressors. 2) The consequences of outbreeding on population fitness and phenotypic plasticity, and 3) The selective effects of fluctuating selective regimes on plasticity genes.

In order to investigate in which way environments fluctuating with different intervals can affect the mean population average fitness, and to quantify the costs and benefits of genetic variability in fluctuating environments, sexually reproducing strains ought to be utilised, creating fluctuating temperature environments and making truncated selection experiments in which the extreme phenotypes at the two tails of the phenotypic distribution are selected away. Important information could in this way be obtained about the extent of the environmental information that will be transmitted to the offspring, and to what extent it can enlarge the plastic response of a trait when selecting for plasticity genes.

6.1.2 Collection and analysis of empirical data

Molecular and quantitative genetics studies should be conducted on several species with different ecological characteristics and with different demographic history, such as recent and ancient population decline or expansion. Changes in population size and range are frequent consequences of CIEC, and examples include habitat fragmentation and rapid colonization or recolonization processes. Extensive collections of several species provide the opportunity to analyse large numbers of samples on a temporal scale and directly document changes in genetic diversity. The results of these analyses will improve our understanding of the historical dimension of population change, and provide important data for the interpretation of genetic diversity studies in an ecological and evolutionary context. The possibility of amplifying ancient DNA from old museum specimen (Pertoldi et al., 2005b), should also be used. Furthermore, a phylogeographic approach should be carried out. The innovative aspect of this approach consists of the fact that different molecular and quantitative genetics techniques should be employed simultaneously.

To document the range of genetically based morphological variation within and among populations, a comparison of the degree of quantitative genetics distance (QST) with neutral genetic distance (FST) should be made (Mckay & Latta, 2002). Comparisons of morphometrical (for example, size and shape) and life-history variability (for example, longevity and fecundity) of populations and their crosses with molecular variability (using microsatellites) could present important information about the influences of environmental and genetic components in a non-genetic-equilibrium situation. Furthermore, it will provide important information about the extent to which crosses between different strains affect the various components of σ^2_p (plasticity, developmental homeostasis, canalization and σ^2_e).

The combination of ecological models of the distribution of the species investigated with both mitochondrial DNA (mtDNA) data and synthetic genetic maps constructed from

multivariate analysis of microsatellites and morphometric data will allow us to discuss hypothesized historical biogeographic scenarios. By directly dating and quantifying changes in genetic diversity, these investigations will allow examination of postulated causes of population decline, including habitat loss and temperature increase.

The genetic data obtained from the investigations mentioned above provides the information on postglacial history as well as on current demographic threats (fragmentation, relict populations, marginal populations; levels of inbreeding). The results of this approach will provide important information about: 1) The genetic consequences of population fragmentation and rapid recolonization caused by climate change. 2) The extent of the genetic diversity of modern populations compared to that in the late Pleistocenic environment, and 3) Pattern of species recolonization in Europe and their response to environmental change after the last glaciation.

6.1.3 Computational population genetics

Stochastic simulation tools, based on a quantitative infinitesimal model, where the size of N_E can be varied, should be developed. In the simulation models, each phenotype should be considered to be the sum of independent genetic components (σ^2_a, dominance and epistasis) and σ^2_e, and the σ^2_p in a population should be described as the sum of independent variances for each of these effects. Several questions could be answered:

1. Understanding how different environmental scenarios can affect both genetic and demographic parameters.
2. Understanding how much difference in life history between ecologically similar species can cause substantial differences in N_E and σ^2_a, and to what degree fluctuations in vital rate parameters induced by environmental change can alter N_E,
3. Quantifying the interactions of each particular life history parameter with other factors (sensitivity analysis), and
4. Quantifying the effects and the interactions that factors such as N_E, inbreeding, gametic phase disequilibrium, plasticity, and developmental homeostasis have on the speed at which a population can react to a selective pressure.

Given that the information obtained from the computational approach can be combined with empirical data, obtained from approaches 6.1.1 and 6.1.2 the model will be a powerful tool for understanding complex dynamics and to make predictions concerning the possible effects of CIEC and their interactions with other factors.

6.2 Expected yield of the multidisciplinary approach

The establishment of such an approach which integrate experimental, theoretical and applied ecological and evolutionary genetics, will create synergistic effects and contribute to the understanding of the consequences of CIEC and the questions addressed will provide important contributions to general ecology and conservation genetics as there is a requirement for detailed studies on how variation at the level of genes translates through developmental and physiological processes, into phenotypic variation for ecologically important traits. Further scientific progress will be achieved by merging and complementing recent efforts in evolutionary and ecological genetics by: 1) Collecting informative genetic and environmental data sets in natural populations and from preserved specimens, 2) Merging taxonomic, ecological and genetic databases, 3) Using

molecular data in combination with quantitative traits and environmental data, and **4)** Unravelling the distribution of variation at functional vs. non-coding sequences in natural populations.

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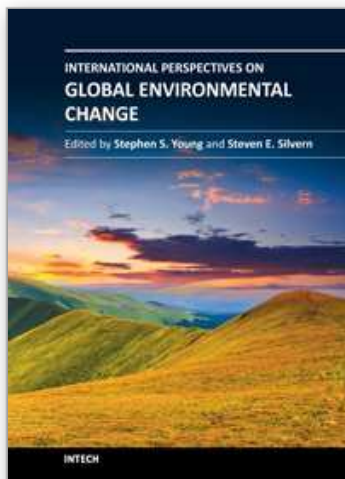
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