ABSTRACT

Consequences of within population variation have recently attracted an increased interest in evolutionary ecology research. Theoretical models suggest important population-level consequences, but many of these predictions still remain to be tested. These issues are important for a deepened understanding of population performances and persistence, especially in a world characterized by rapid fragmentation of natural habitats and other environmental changes.

I review theoretical models of consequences from intra population genetic and phenotypic variation. I find that more variable populations are predicted to be characterized by broader resource use, reduced intraspecific competition, reduced vulnerability to environmental changes, more stable population dynamics, higher invasive potential, enhanced colonization and establishment success, larger distribution ranges, higher evolvability, higher productivity, faster population growth rate, decreased extinction risk, and higher speciation rate, compared with less variable populations.

To test some of these predictions I performed experiments and compared how different degree of colour polymorphism influences predation risk and establishment success in small groups. My comparisons of predation risk in mono- and polymorphic artificial prey populations showed that the risk of being eaten by birds does not only depend on the coloration of the individual prey item itself, but also on the coloration of the other members of the group. Two experiments on establishment success in small founder groups of *Tetrix subulata* pygmy grasshoppers with different degree of colour morph diversity show that establishment success increases with higher degree of diversity, both under controlled conditions in outdoor enclosures and in the wild. These findings may be important for re-stocking of declining populations or re-introductions of locally extinct populations in conservation biology projects.

I report on remarkably rapid evolutionary shifts in colour morph frequencies in response to the changed environmental conditions in replicated natural populations of pygmy grasshoppers in fire ravaged areas. This finding

illustrates the high adaptive potential in a polymorphic species, and indicates the importance of preserved within-species diversity for evolutionary rescue.

Finally, I review if theoretical predictions are supported by other published empirical tests and find strong support for the predictions that more variable groups benefit from reduced vulnerability to environmental changes, reduced population fluctuations and extinction risk, larger distribution ranges, and higher colonization or establishment success.

In conclusion, my thesis illustrates how within-population variation influences ecological and evolutionary performances of populations both in the short and long term. As such, it emphasizes the need for conservation of biodiversity also within populations.

Key words: colour polymorphism, diversity, establishment success, evolutionary changes, population-level consequences, predation risk, *Tetrix subulata*, variation.

To Ellika, Magdalena and Elias,
My Love, my Joy

To see a world in a grain of sand,
and a heaven in a wild flower,
hold infinity in the palm of your hand,
and eternity in an hour.

W. Blake

LIST OF PAPERS

The thesis is based on the following original papers, which are referred to in the text by their Roman numerals. Papers I -V are reprinted with kind permissions from the publishers.

I. **Wennersten, L.** and Forsman, A. (2012) Population-level consequences of polymorphism, plasticity and randomized phenotype switching: a review of predictions. Biological Reviews 87: 756-767.

II. **Wennersten, L.** and Forsman, A. (2009) Does colour polymorphism enhance survival of prey populations? Proceedings of the Royal Society B 276: 2187–2194

III. **Wennersten, L.**, Johansson, J., Karpestam, E. and Forsman, A. (2012) Higher establishment success in more diverse groups of pygmy grasshoppers under seminatural conditions. Ecology, in press, pre-print available at http://dx.doi.org/10.1890/12-0550.1.

IV. Forsman, A., **Wennersten, L.**, Karlsson, M. and Caesar, S. (2012) Variation in founder groups promotes establishment success in the wild. Proceedings of the Royal Society B 279: 2800-2806.

V. Forsman, A., Karlsson, M., **Wennersten, L.**, Johansson, J. and Karpestam, E. (2011) Rapid evolution of fire melanism in replicated populations of pygmy grasshoppers. Evolution 65: 2530-2540

VI. **Wennersten, L.** and Forsman, A. Strong support for predicted population-level consequences of diversity: a review of experimental and comparative studies. Manuscript.

SVENSK SAMMANFATTNING

Betydelsen av ärftlig inomartsvariation för populationers eller arters anpassning på lång sikt har varit känd sedan Darwin (1859). Det beror på att selektionen, den viktigaste evolutionära kraften, aldrig skapar egna lösningar utan bara sorterar ut de bäst anpassade individerna bland de alternativ som finns tillgängliga. Till skillnad från långsiktiga evolutionära förändringar, är inomgrupps-variationens betydelse för gruppens ekologiska framgång i ett kortare perspektiv, betydligt mindre undersökt. I en föränderlig värld, där naturliga miljöer i rask takt exploateras och fragmenteras och där klimatförändringar, föroreningar och andra miljöförändringar i hög grad påverkar populationers och arters chanser till anpassning och fortlevnad, blir dessa frågor ytterst viktiga.

Flera teoretiska modeller har publicerats med förslag på hur inomartsvariationen kan tänkas påverka populationer på kort och lång sikt. Jag gjorde en litteraturgenomgång (Paper I) för att sammanställa sådana teoretiska modeller och fann en hög grad av samstämmighet mellan olika förutsägelser, men också att flera av dem sällan testats empiriskt. Jag genomförde därför experiment för att pröva några av förutsägelserna.

Jag undersökte om färgen på konstgjorda byten, liknande fjärilslarver, påverkade deras risk att bli uppätna av fåglar (Paper II). Jag fann att inte bara färgen på enskilda byten, utan även färgen på andra individer i samma grupp, påverkar bytenas risk att bli uppätna.

I två experiment testade jag hur grupper av färg-variabla torngräshoppor klarar att etablera sig i nya miljöer. I båda experimenten jämförde jag etableringsframgången mellan grupper med olika grad av variation och fann att mer variabla grupper har lättare att etablera sig och föröka sig på nya platser. Detta gäller både då jag genomförde experimentet under kontrollerade former i utomhusburar (Paper III) och då jag satte ut små grupper av gräshoppor i nya miljöer i fält (Paper IV).

I en långtidsobservation av flera olika populationer i olika miljöer undersökte jag hur samma art av torngräshoppa anpassade sig till den omfattande miljöförändring som en skogsbrand utgör. Jag fann att andelen

mörka gräshoppor var betydligt högre på brända områden än på icke brända, men även att andelen mörka individer snabbt sjönk vartefter att vegetationen återkoloniserade området de närmaste åren efter branden. Denna studie visar på en hög grad av anpassningsförmåga hos denna färg-variabla art, men indikerar också att förekomsten av flera varianter inom samma population antagligen var en förutsättning för denna snabba evolutionära förändring.

Slutligen gjorde jag en litteraturgenomgång för att undersöka i vilken grad de teoretiska förutsägelserna har stöd i annan publicerad empirisk forskning. Denna genomgång visade på en mycket stor samstämmighet hos de empiriska studier som undersökt effekterna av inomartsvariation. I nästan samtliga fall redovisar studierna att mer variabla grupper är mindre sårbara för miljöförändringar, uppvisar mindre fluktuationer i populationsstorlek, lägre utdöenderisk, större utbredningsområde och högre etableringsförmåga, jämfört med mindre variabla grupper.

Jag argumenterar för att avhandlingens resultat är av betydelse dels för naturvården, t.ex. i bevarandebiologiska projekt som vid återutplanteringar av hotade arter, dels för en fördjupad förståelse av inomartsvariationens betydelse för populationer, ekologiskt och evolutionärt. Där menar jag att min avhandling illustrerar vikten av bevarad biodiversitet inom populationer och arter.

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Introduction

Biodiversity is not only the variety among species, but also diversity of ecosystems and diversity within species, according to The Convention on Biological Diversity from UN (1993). Within species diversity includes genotypic (the genetic makeup) and phenotypic (the individual expression as a result from the interaction of genes and environment) differences between individuals or groups of individuals. The role of heritable within-species variation for adaptation and evolution has been well recognized since Darwin (1859). How phenotypic variation among individuals influences the ecology of populations is a far less explored, but currently expanding area of research. It has been argued that within-population variation often is an underestimated issue in ecological models (Bolnick et al. 2011). My thesis concerns how differences among individuals influence the populations they are part of. First, I review predictions from theoretical models concerning population-level consequences of within-species variation. I report an overall agreement in many respects, but also how predictions sometimes differ due to conditions of the organism, the environment, or source of variation. Then I experimentally investigate whether predation risk is lower in polymorphic compared to monomorphic artificial prey populations, and if and how establishment success in groups of pygmy grasshoppers is influenced by degree of variation in the founder group. I also perform a field study to examine how natural populations respond to spatiotemporal environmental changes. Finally, I review empirical studies that used either an experimental or comparative approach to test predictions on population-level consequences of variation generated by theory, and I also discuss implications and suggest directions for future research.

Different modes of phenotypic variation and determination

Among individual variation may be discrete or continuous, genetic or environmentally controlled (Fig. 1). Discrete variation, with no or little variation within phenotypic classes (Fig. 2iii, e.g., sex, or castes in social insects), is called polymorphism if genetically determined and polyphenism if environmentally induced (Fig. 1), but may also be a result of both genetic and environmental factors. Continuous variation (Fig. 2i and ii, e.g., body-size) may be genetically determined, influenced by environmental factors, or (probably most often) reflect a combination of genes and environmental influences.
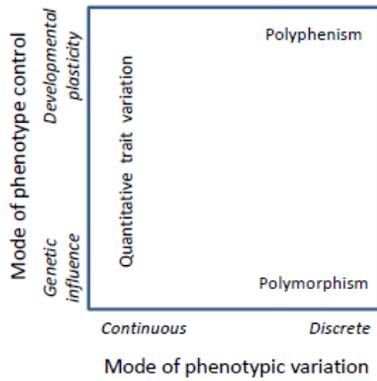
Figure 1. Classification of phenotypic variation according to mode of variation (continuous or discrete) and mode of phenotype control (genetic influence or developmental plasticity). There is a continuum ranging from discrete variation in the form of two distinct phenotype classes to fully continuous trait-value distributions displayed by quantitative traits. Phenotypic variability may be affected by a combination of genetic and environmental influences on developmental processes, and there is a continuum that ranges from traits with a strictly genetic control, via equal contribution of genetic and environmental cues to traits that are primarily influenced by developmental plasticity in response to non-genetic environmental cues. (Paper I)
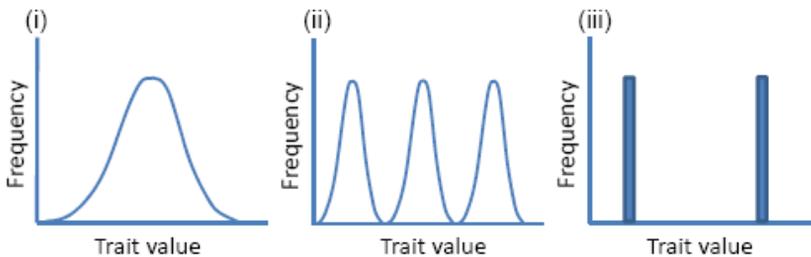
Figure 2. Continuum of phenotype frequency distributions ranging from (i) continuously varying traits, over (ii) multimodal traits with continuous variation within each category to (iii) discrete traits with no or little variation within each phenotype class. Traits with a monomorphic and strictly invariable mode of phenotype distribution are probably very rare, because given that measurements are made with sufficiently high resolution, there will usually exist variation due to noise in the form of environmentally induced perturbations of developmental pathways. (Paper I)

What determines phenotypes?

a) Polymorphism

Ford (1940) defines polymorphism as "the occurrence together in the same habitat of two or more discontinuous forms, or "phases", of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation or immigration." This definition excludes continuous traits, ephemeral, mutated individuals (Ford 1940), but also ecotypes, that is locally adapted populations found in different environments (Pigliucci 2001).

The different forms can either be easily distinguished, like the two sexes in many animal species, or different discrete colour morphs in some species, or be less obvious, at least to the human eye. An example of such a less apparent polymorphism is the different blood groups in humans. Regardless whether the polymorphism is readily observable, the genetic determination of polymorphism (Fig. 1) is important for evolutionary and ecological consequences of the variation. A polymorphic population may include substantial genetic heterogeneity that is apparent at the phenotypic level and thus available for selection (Fig. 3i), while plasticity may generate phenotypic monomorphism and hide genetic variation (Fig. 3ii). The latter may be an effect of canalization, a buffering effect that may conceal genetic heterogeneity from selection and store it in the genome for generations (Dworkin 2005). Plasticity may also induce phenotypic variation in a genetically homogenous population if individuals develop under different environmental conditions and respond to particular cues in the environment. The observed differences among phenotypes may in this case hide a genetic homogeneity for the specific trait (Fig. 3iii).

i) genetic polymorphism:

Environment:	1, 2 or 3	1, 2 or 3	1, 2 or 3
Genotype:	AA	Aa	aa
Phenotype:	I	II	III
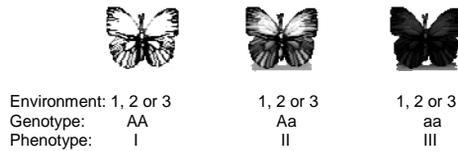
ii) phenotypic homogeneity due to developmental plasticity:

Environment:	1	1	1
Genotype:	AA	Aa	aa
Phenotype:	II	II	II
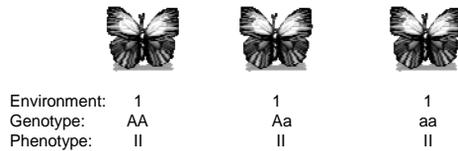
iii) polyphenism due to developmental plasticity:

Environment:	1	2	3
Genotype:	Aa	Aa	Aa
Phenotype:	I	II	III
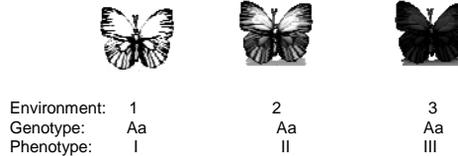
Figure 3: Illustration of simulated situations with genetic polymorphism and developmental plasticity. In i) the observed differences among phenotypes I, II and III reflect genetic polymorphism, but no plastic response due to different environmental conditions. In ii) an observed homogeneity among phenotypes hides genetic variation, due to developmental plasticity with the same response from different genotypes when exposed to the same environmental conditions. In iii) an observed difference between phenotypes hides a genetic homogenous group due to developmental plastic responses under different environmental conditions.

Polymorphism is not restricted to morphological traits, but exists also in behaviour and life history traits, like different mating strategies or different foraging patterns among individuals in a population.

b) Plasticity

For most phenotypic traits, variation among individuals is a result of both the specific genotype and the environment. The reaction norm of genotypes describes the relationship between environments and phenotypes (Pigliucci 2001). Plasticity is an attribute of the reaction norm in which the expressed phenotype changes along a specific environmental gradient (Fig. 4b-c) (Pigliucci 2001). If a specific genotype expresses the same phenotype across a gradient of

an environmental factor (e. g., temperature, light, pH), this genotype is said to have a non-plastic reaction norm, that is, a zero slope in the phenotype-environment relationship (Fig. 4a) (Newman 1992). Plastic responses may be continuous (Fig. 4b) or stepwise (i.e., threshold responses) (Fig. 4c). Threshold responses may result in discrete distinguishable phenotypes in polyphenic populations (Fig. 2iii), like different castes in social insects, alternative seasonal forms in insects (Nijhout 2003), or heterophylly in plants; the ability of some vascular plants to form different leaves above and below the water surface (Bruni et al. 1996, Pigliucci 2001).

Sometimes, plastic responses result in similar phenotypes, despite genotypic differences. Stabilizing selection may have this effect on phenotypes with different genetics (Bradshaw 1965). Such observed phenotypic homogeneity in a population can hide a genetic heterogeneity (Fig. 3ii). Conversely, individuals with similar genetic make-up may express different phenotypes if they have developed under different environmental conditions, due to plastic responses (Fig. 3iii).
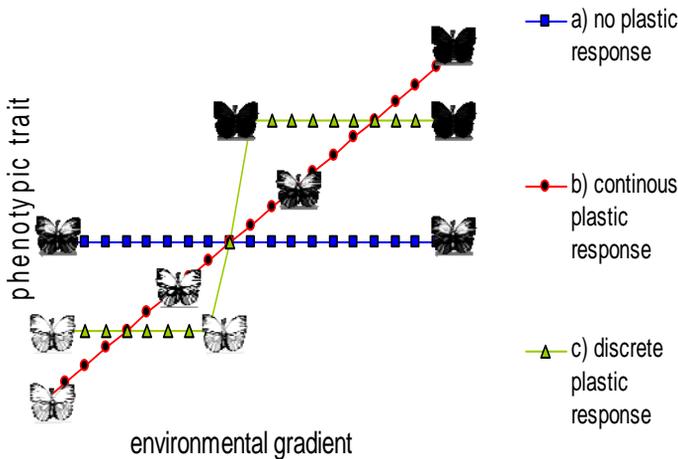
Figure 4: Different reaction norms in a simulated situation with phenotypes expressing a specific trait (degree of melanism), across a gradient of an environmental factor, x. Reaction norms of type a) show no plasticity: the expressed phenotypes are the same, regardless of the different levels of the environmental factor x. Reaction norms of type b) show plasticity with continuous variation: expressed phenotypes show a higher degree of melanism with an increased level of the environmental factor x. Reaction norms of type c) show plastic responses with discrete variation (threshold response) to the environmental factor x, where a low level of the environmental factor x results in a light morph and a high level result in a darker, melanistic morph.

Even if plasticity is widespread in both plants and animals, there are some important differences between modular (as plants) and unitary (as most animals) organisms (Paper I). In unitary organisms, plastic responses are more often integrated in the whole organism, due to the central nervous and endocrine control system (Sultan and Stearns 2005). In modular organisms, such as plants, a plastic response may instead be restricted only to some parts of the organism and is also possible during the whole lifetime (Paper I). In unitary organisms, on the other hand, developmental plasticity may be possible responses early in the life-cycle, while physiological or behavioural plasticity may be more important responses after the development is completed.

c) Randomized switching

A third source of within-species variation is randomized switching, also termed bet-hedging, where the variation is due to randomly variable offspring (Seger and Brockmann 1987, Philippi and Seger 1989).

In polymorphic populations, different morphs may encounter a higher fitness in different environments, due to differences in the selection regime. If one particular morph is superior under most conditions, this morph will soon outcompete the others and the population will transform into monomorphism (Ford 1945, Moran 1992, Brisson et al. 2006). Polymorphism may thus result in a high variance for individual fitness in populations, due to current environmental conditions, but reduced variance for fitness at the population level (Seger and Brockmann 1987). Bet-hedging may instead reduce variance in individual fitness, but at the cost of a lower mean fitness at the population level (Seger and Brockmann 1987, Philippi and Seger 1989). Bet-hedging is most likely to evolve in unpredictable temporal changing environments where the variation scale is longer than one generation, and less likely in spatially heterogenic environments (Seger and Brockmann 1987, Philippi and Seger 1989, West-Eberhard 2003, Leimar 2009). In annual desert plants, species that experience greater variation in per capita reproductive success when germinating, have a lower average germination fraction, compared to other species in the same habitat (Venable 2007). Thus, a bet-hedging strategy in germination enhances the chance for some of the seeds to germinate under beneficial conditions, for instance, with higher precipitation. This reduces the long-term risk at the cost of short-term success (Venable 2007).

d) Integrated phenotypes

Obviously, a clear distinction between polymorphism and plasticity, as presented above, is an oversimplification. Since different reaction norms among individuals are due to genetic differences (Pigliucci 1996), and since genetically encoded hormones and enzymes may play central roles in genotype-environment interactions (Pigliucci 2001), plasticity itself may be viewed as a special form of polymorphism (Pigliucci 2001, West-Eberhard 2003, Paper I). In addition,

genetically controlled polymorphic traits may exhibit a certain degree of plasticity (Paper I), and polymorphism has been suggested to represent a special case of phenotypic plasticity (Leimar 2005). Furthermore, it has been argued that phenotypic variants may be induced both by environmental and by allelic variation (i.e., inchangeability) (West-Eberhard 2003, Leimar 2009). Leimar (2009) argues that the different allele frequencies in different proportions of the population may inform about coming selective regimes, in a way parallel to information from environmental cues. In this perspective, polymorphism and plasticity are almost inseparable, and should be interpreted within a common framework (Agrawal 2001, Pigliucci 2001, West-Eberhard 2003, Pigliucci and Preston 2004, Jablonka and Lamb 2006, Leimar et al. 2006, Leimar 2009). In spite of this notion, I argue that it is sometimes both possible and meaningful to distinguish polymorphism from plasticity (Paper I).

Selection acts on phenotypes, but a genetic coupling is necessary for heritability and thus for an evolutionary change by response to selection to occur.

Population-level consequences

My thesis focuses on population-level consequences of variation among individuals. In recent years, the multi-level selection theory has received a renaissance, after decades of rejection (Sober and Wilson 1998, Keller 1999, Wilson 2004, Okasha 2006, Wilson and Wilson 2007, Wilson et al. 2008). Multi-level selection theory of today reject the naïve idea from the past that things may evolve for the best of the group or the best of the species (Wynne-Edwards 1962), but state that selection occurs on the variation that is present at different levels of organization; at the level of individuals within populations as well as among populations (Sober and Wilson 1998, Okasha 2006, Wilson and Wilson 2007). Selection is nothing but a sorting process favouring higher fitness to lower. For individual traits selection sorts among individuals, for population characteristics selection sorts among populations (Sober and Wilson 1998). Diversity in groups is a population-level characteristic that may influence the fitness of the group. For selection to act at the group level, there has to be a variation among groups for the trait in focus, and also fitness consequences of this trait for the group (Sober and Wilson 1998). This is parallel to evolution of individual traits due to differences in individual fitness. What Sober and Wilson (1998) state is that for evolution by selection to occur at a specific level, selection must act at the same level, irrespective of whether it is lower or higher than the level of individuals. In my thesis I address neither evolutionary origin nor maintenance of traits, rather I investigate consequences of within-population variation and compare performance in homogenous *versus* heterogeneous groups.

Beneficial effects of diversity

Beneficial effects of diversity have been characterized into additive and non-additive effects (Fig. 5), both among individuals at the population-level (Hughes et al. 2008, Agashe 2009) and among species at the level of ecosystems (Vanelslander et al. 2009). Additive effects are statistical mechanisms from the number of alternatives. With additive effects a diverse group is expected to perform the sum of what included genotypes perform in monocultures (Hughes et al. 2008). The sampling effect is an additive effect, a higher probability in a more diverse group to include phenotypes with high fitness under the current selection regime (Forsman et al. 2008, Hughes et al. 2008). A sampling effect (Fig. 5) may lead to replacement (selection effect or selection sweep) if a superior genotype performs better and outcompetes alternative genotypes in a poly-culture (Bell 1991, Hughes et al. 2008, Hughes and Stachowicz 2011). Which genotype that turns out to be superior depends on the selection regime (Jump et al. 2009). Genetic and phenotypic diversity also facilitates adaptation to changed conditions, that is, an evolutionary rescue effect (Bell and Collins 2008, Bell and Gonzalez 2009), or, result in new combinations of traits in the next generation from recombination in sexually reproducing organisms (Barton and Charlesworth 1998).
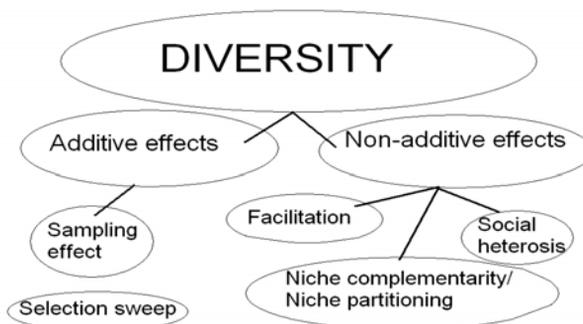
Figure 5: Beneficial effects of among individual diversity at the population level within species (Hughes et al. 2008, Agashe 2009), or, among species at the ecosystem level (Vanelslander et al. 2009). Effects can be characterized as additive (effects from higher numbers of alternatives) or non-additive (complementary effects beyond the number of alternatives). Facilitation, niche partitioning or niche complementarity, and social heterosis are all non-additive effects. The mechanisms behind non-additive effects may be due to reduced competition when alternatives show different preferences, to beneficial effects from some of the alternatives for some others, or to mutualistic interactions among alternatives. A selection sweep is an effect from selection if one of the alternatives outcompetes the others. The superior alternative could be either one included from the beginning (from the sampling effect), or from a new alternative that in itself is the result from diversity (complementarity effect), for instance by recombination in sexually reproducing organisms.

Non-additive effects are more than the sum of the included alternatives. This category includes facilitation, niche complementarity or niche partitioning, and social heterosis (Fig. 5). Facilitation occurs when diversity in one group promotes diversity in another (Gamfeldt et al. 2005, Vellend 2008), or when one species modifies the environment in a way that is beneficial for other species (Vanelslander et al. 2009). The niche complementarity hypothesis suggests genotypic complements to benefit the population. This is an advantage of variation *per se*, rather than inclusion of morphs with high fitness (Reusch et al. 2005). Differential utilization of resources by specialized morphs may decrease intra-specific competition (Forsman et al. 2008) and enable higher population densities (Tinker et al. 2008, Caesar et al. 2010).

Closely related to niche complementarity is the hypothesis of social heterosis (Nonacs and Kapheim 2007, Nonacs and Kapheim 2008). Nonacs and Kapheim (2007, 2008) suggest genetic diversity to be maintained in populations due to benefits from interacting individuals in genetically heterogeneous groups. The beneficial effect of genetic diversity is potentially powerful when the optimal phenotype can not be expressed by any single individual (Nonacs and Kapheim 2007). This is the case for instance in contradictory traits like shy and bold, fast and slow, where occurrence of both traits in a population may be beneficial for the group (Nonacs and Kapheim 2007).

Replacement of alternatives by one superior morph due to a selection effect (selection sweep), may occur also from non-additive effects, for instance in sexually reproducing species where higher genetic diversity in the population may result in new combinations of traits during recombination (Agashe 2009).

Aims

From causes to consequences of phenotypic variation

There is an extensive literature on the evolutionary origin and maintenance of within species variation (e.g., Ford 1940, Dobzhansky 1951, Ford 1965, Hedrick 1986, Moran 1992, West-Eberhard 2003, Einum and Fleming 2004, Hedrick 2006, Beaumont et al. 2009), while the consequences of variation for populations, species and eco-systems have received a limited, but currently growing interest (Sultan 2000, Agrawal 2001, Pigliucci 2001, Meyers and Bull 2002, Sultan 2004, Miner et al. 2005, Forsman et al. 2008, Hughes et al. 2008). My thesis mainly concerns how phenotypic variation and polymorphism with a genetic underpinning in ecologically important traits, especially colour polymorphism, influences population performances. In my thesis, I review literature (Paper I and VI), perform experiments (Paper II-IV), and report on long-term observations of natural populations (Paper V), to explore effects of within species variation at the population-level. In the review of theoretical models (Paper I) the approach is a broad synthesis of predicted evolutionary and ecological consequences of within-population variation from different sources (i.

e., polymorphism, plasticity and randomized switching). In the experiments I focus on colour polymorphism and investigate if predation risk is reduced for more variable groups (Paper II), if morph diversity enhances establishment success in the model system of pygmy grasshoppers under controlled conditions in outdoor enclosures (Paper III) and under natural conditions in the wild (Paper IV). In the long-term observational study, I report on rapid evolutionary responses to changing environments in this polymorphic model species (Paper V). Finally, I review experimental and comparative studies to examine whether there is empirical support for the predicted population-level consequences of variation (Paper VI).

I focus on the following questions:

A. How, according to theory, is within group diversity predicted to influence population dynamics, extinction risk, colonization, vulnerability to environmental changes and evolvability? How, if at all, are predictions dependent on the source of variation; polymorphism, plasticity or randomized switches?
B. How do more diverse colour polymorphic groups respond to predation rate, compared to less variable groups?
C. How does within-group diversity influence establishment success in small founder groups?
D. How do polymorphic populations respond to rapid environmental changes under natural conditions?
E. To what extent are predicted population-level consequences of variation supported by results from previous experimental and comparative studies?

POPULATION-LEVEL CONSEQUENCES OF VARIATION

Review of predictions on population-level consequences of variation (Paper I)

When effects of within species variation for population processes have been studied, this has typically addressed one specific source of variation (plasticity (Sultan 2000, Agrawal 2001, Pigliucci 2001) or polymorphism (Forsman et al. 2008, Hughes et al. 2008)), or considered one specific aspect of population performance, such as rate of speciation (Gray and McKinnon 2007, Krüger 2008, Pfennig et al. 2010). In Paper I, I review those theoretical models I am aware of that consider ecological consequences of within population variation, and ask how and in what ways within group diversity influences population prospects such as population dynamics, establishment success and evolvability. I also examine if consequences of variation are suggested to be similar if caused by genetic polymorphism, developmental plasticity or randomized switching (Paper I). I report that, overall, theoretical models of consequences of within population variation due to genetic polymorphism , or to developmental plasticity, concur that more variable populations should be associated with broader resource use, reduced intraspecific competition, reduced vulnerability for environmental changes, more stable population dynamics, higher invasive potential, improved dispersal and colonization potential, larger distribution ranges, higher evolvability, higher productivity and population growth rate, decreased extinction risk, and higher speciation rate (Sultan 2000, Agrawal 2001, Pigliucci 2001, Forsman et al. 2008, Hughes et al. 2008, Paper I, Table 1). Among the twelve predictions reported on in Paper I, I selected those intimately associated with population persistence under rapidly changing conditions namely; stability in population, establishment success, and evolutionary response, which I first briefly outline below, but also test empirically in Papers II-V, and finally review in other empirical studies (Paper VI).

Table 1: Comparison of predictions from theoretical models of population-level ecological and evolutionary consequences of phenotypic variation caused by genetic polymorphism (Forsman et al., 2008; Hughes et al., 2008), developmental plasticity (Agrawal, 2001; Pigliucci, 2001; Sultan, 2000) and for purely randomized switching (proposed in Paper I). Proposed mechanisms are provided in parenthesis under each prediction. Increase or decrease indicates whether phenotypic variation has been hypothesized to result in increased or decreased performance relative to a less-variable population. Equal indicates no change relative to a less-variable population. Consequences may differ depending on whether the environment is fine-grained or coarse-grained, whether organisms are modular or unitary and mobile or sessile, and whether traits are flexible or fixed. In some cases, the consequence of plasticity conforms to that of genetic polymorphism because reaction norms vary among genotypes, such that the effect is due to polymorphism rather than to plasticity per se.

Population-level ecological or evolutionary response	Sources of variation		
	Genetic polymorphism Forsman *et al.* (2008)[1] Hughes *et al.* (2008)[2]	Developmental plasticity Agrawal (2001)[3] Sultan (2000)[4] Pigliucci (2001)[5]	Purely randomized switching Suggested in Paper I
Niche breadth of population	Increase[1] (individual specialists)	Increase[4] (intra-individual generalists in modular organisms or flexible traits, or individual specialists in fine-grained environments)	Increase (individual specialists)
Intra-specific competition	Decrease[1,2] (resource partitioning)	Decrease [Paper I] (resource partitioning in fine-grained environments)	Decrease (resource partitioning)
Vulnerability to environmental changes	Decrease[1,2] (variation available for selection and existence of pre-adapted phenotypes)	Decrease[4,5] (for flexible traits or if changes in selection regimes are predictable and not too sudden)	Decrease (buffering effect of variation and pre-adapted phenotypes)
Fluctuations in population size	Decrease[1,2] (buffering effect of variation and pre-adapted phenotypes)	Decrease [Paper I] (for flexible traits or if environmental changes are predictable and not too sudden)	Decrease (buffering effect of variation and pre-adapted phenotypes)

Colonization and establishment	Increase[1] (variation in requirements and existence of pre-adapted phenotypes)	Increase[3,4] (but time lag for irreversible traits may result in establishment failure)	Increase (variation in requirements and existence of pre-adapted phenotypes)
Invasiveness	Increase [Paper I] (existence of pre-adapted phenotypes and variation available for selection)	Increase[3,4] (adjustment of phenotypes to local conditions followed by genetic assimilation)	Equal (no local adaptation because variation not heritable)
Distributional range size	Increase[1] (existence of pre-adapted phenotypes and variation available for selection and evolution)	Increase[3,4] (adjustment of phenotypes to local conditions followed by genetic assimilation)	Increase (variation in requirements and existence of pre-adapted phenotypes)
Evolutionary potential	Increase[1,2] (heritable phenotypic and genetic variation available for selection)	Increase[3,5] / Decrease [5] (release *versus* masking of cryptic genetic variation)	Equal (variation not heritable)
Productivity in population	Increase[2] (resource partitioning and buffering effect of variation)	Increase [Paper I] (resource partitioning and buffering effect of variation in fine-grained environments)	Increase (resource partitioning and buffering effect of variation)
Population growth rate	Increase[2] (resource partitioning and buffering effect of variation)	Increase [Paper I] (resource partitioning and buffering effect of variation in fine-grained environments)	Increase (resource partitioning and buffering effect of variation)
Extinction risk	Decrease[1] (different requirements and variation available for selection and adaptation)	Decrease[4] (different requirements in fine-grained environments, asynchronous dynamics across populations in coarse-grained environments)	Decrease (buffering effect of variation and pre-adapted phenotypes)
Rate of speciation	Increase[1] (heritable variation available for selection and assortment of genotypes)	Increase[3] / Decrease[4,5] (release of cryptic genetic variation, genetic assimilation, assortment of genotypes *versus* masking of genetic variation)	Equal (variation not heritable)

a) Predicted higher stability in population dynamics in more variable populations

Small populations are more vulnerable to stochastic density declines (e.g., Smith 1989, Bell and Gonzalez 2009). Theoretical models predict more variable groups to show reduced fluctuations in population dynamics (Forsman et al. 2008, Hughes et al. 2008, Table 1, Paper I). Diversity may enhance stability because of a sampling effect (Fig. 5) that may be particularly important in polymorphic systems where differently specialized morphs represent alternative combinations of functionally and ecologically important traits. For instance in the highly colour polymorphic pygmy grasshoppers, colour patterns co-vary with thermal physiology, reproductive life-history traits, body size, predator avoidance behaviour, microhabitat utilization and diet (Forsman 1995, Forsman and Appelqvist 1998, Forsman 1999c, a, b, 2000, Forsman et al. 2002, Ahnesjö and Forsman 2003, 2006, Karpestam and Forsman 2011). Co-variation of colour pattern with other ecologically important traits is not unique to pygmy grasshoppers. McKinnon and Pierotti (2010) report in their review that colour morphs are associated with other traits in a wide range of organism groups such as arthropods, birds, fish, reptiles, molluscs, and mammals. Traits may be correlated for instance when hormonal profiles influence both colour pattern and other traits (True 2003, McKinnon and Pierotti 2010). If correlational selection promotes genetic couplings between loci, co-variation of traits is probably more frequent when traits are genetically determined; that is, in polymorphic rather than in plastic systems. On the other hand, plasticity may result in co-variation of traits if the same cue influences development of more than one trait. If plasticity results in different ability among individuals to cope with the new conditions, especially for flexible traits or if changes in selection regimes are predictable and not too sudden, plasticity may similarly result in higher population stability in more variable populations (Table 1). For variation resulting from randomized switches, I suggest in Paper I a similar buffering effect on fluctuations in population dynamics due to variation among phenotypes and pre-adapted individuals.

Since population dynamics influences extinction risk (Lande 1993) it is reasonable to expect that more variable groups with more stable population dynamics also are less vulnerable to extinction (Table 1, Paper I and VI).

b) Predicted higher colonization and establishment capacity in more variable populations

The theoretical models reviewed in Paper I concur that colonization and establishment capacities should be enhanced in more variable populations (Table 1), both when variation is due to genetic polymorphism (Forsman et al. 2008) and when it reflects developmental plasticity (Sultan 2000, Agrawal

2001). I suggest a similar effect in variable groups where diversity is due to randomized switches (Table 1, Paper I). For polymorphic species a higher establishment success in more variable groups could be due to a sampling effect, because more variable groups are more likely to include pre-adapted phenotypes (Forsman et al. 2008), or to niche complementarity (Forsman et al. 2008, Bolnick et al. 2011). In an experiment where establishment success was tested in groups of *Balanus improvisus* barnacle larvae with different degree of genotypic diversity, establishment success was positively associated with higher degree of diversity (Gamfeldt et al. 2005). The authors suggest the mechanism behind the higher establishment success in more diverse groups to be due to effects of either facilitation or complementarity (Gamfeldt et al. 2005). A higher establishment success in organisms with a plastic reaction norm may be due to expression of potentially beneficial traits in response to conditions in a novel habitat (Agrawal 2001).

c) Predicted higher capacity to adapt to changing conditions in more variable populations

The two models on genetic polymorphism, reviewed in Paper 1, suggest more variable groups to have higher evolutionary potential (Forsman et al. 2008, Hughes et al. 2008) and two of the models on developmental plasticity concur (Agrawal 2001, Pigliucci 2001). However, Pigliucci argues that plastic reaction norms may either accelerate or slow down the evolutionary response to selection (Pigliucci 2001).

Obviously, the rate of evolutionary response is not the same as the capacity for adaptive evolutionary changes. Diversity may be important for both. Plasticity is an individual possibility to adapt the phenotype according to environmental conditions, therefore, a population where individuals are capable to adaptive plastic responses may improve the chances for the population to persist during stressful environmental changes and thereby give time for adaptation to the new conditions (Sultan 2000). Polymorphism, on the other hand, is by definition a population character, and phenotypic diversity itself may be beneficial in the short term (Fig 5), while the capacity for adaptation to changed conditions in the longer term depends on the standing genetic variation in the population. These alternative mechanisms are discussed further below (Paper V).

When the source of variation is randomized switches, I suggest evolutionary potential not to differ substantially between groups of high or low diversity, due to lower heritability in such systems compared to polymorphism or plasticity (Paper I).

d) Conclusions from the review of predictions

The review of predictions of consequences of within population variation revealed agreements for a range of predictions, but also that many predictions

still remain to be tested. Below, I report on a series of experiments carried out to examine whether predation risk is reduced in polymorphic compared with monomorphic populations (Paper II), whether establishing success is higher in founder groups with higher degree of variation, under semi-natural conditions (Paper III), and in the wild (Paper IV). I also report on rapid evolutionary responses of colour morph frequencies in natural populations in the face of changing conditions (Paper V).

Does polymorphism reduce predation risk in prey populations (Paper II)?

Does the fitness of an individual depend only on its own characteristics, or also on the characteristics of the group the individual is part of (Okasha 2006)? It has been suggested that colour polymorphism could protect prey populations from predation (Poulton 1890, Croze 1970, Allen 1988, Knill and Allen 1995, Glanville and Allen 1997). Several protective mechanisms have been proposed, among them conservative choice of prey by predators (Allen 1984, Marples et al. 1998, Bond and Kamil 1999), or searching image (i.e., predators focusing on one type of prey at a time), (Croze 1970, Allen 1988, Bond and Kamil 1998). The searching image could give an individual prey item a higher chance of protection in a polymorphic population if the predator is not familiar with the specific type of prey (Glanville and Allen 1997). Predation in polymorphic prey populations may also be inefficient due to longer processing information time (Allen 1988). Another suggested protective mechanism is that predators may perceive prey densities in polymorphic populations to be lower than they actually are (Croze 1970). The latter argument could allow a polymorphic population to increase in density without increasing the risk of predation (Croze 1970). In spite of the long history of the proposed decreased risk of predation in polymorphic compared with monomorphic populations (Poulton 1890), the hypothesis has very rarely been empirically tested. There are only very few studies that compare predation in mono- and polymorphic prey populations, and most of these studies use digital prey items on a screen and with humans acting as predators (Knill and Allen 1995, Glanville and Allen 1997). I am aware of one study only that had a more ecologically realistic design, with wild crows predating mussel shells of different colours, hiding a piece of meat as reward (Croze 1970). Even if the latter experiment documented a protective effect of polymorphism, it must be interpreted with caution since one single pair of crows was used in all replicates of the study (Croze 1970).

In 2008, I compared survival of mono- or polymorphic artificial prey populations. I also compared the risk of predation for individual prey items of different colours when they were included in monomorphic or polymorphic populations, respectively (Paper II). I aimed for an ecologically realistic design

with wild birds as predators under natural conditions in the field, because foraging behaviours of free-living birds may differ from those of captive birds in aviaries (Thomas et al. 2004). However, as prey items I decided to use artificial pastry baits, made of a dough of butter and flour and coloured with food colouring in four different colour variants; yellow, red, green and brown (see Paper II for details). I formed the dough into 20 mm long cylinders, resembling Lepidoptera larvae, and presented them to birds in the wild in groups of 12 items, resembling small family groups of larvae. The pastry baits were placed on tree trunks, in splits in the bark, or nailed to the upper surface of twigs. Each replicate consisted of 8 populations with 12 prey items in each. Four of the populations in each replicate were monomorphic (one of each of the four colours) and four were polymorphic (each including three items of each colour). In total I used 2976 prey items, organized into 31 replicates of 8 populations each.

There was a significant effect of colour on estimated mean survival time for both populations and individual baits. Contrary to predictions, polymorphic populations did not survive the longest. Instead, polymorphic populations survived shorter time than monomorphic green populations, and did not significantly differ in survival time from monomorphic red, yellow, or brown populations (Fig. 6).
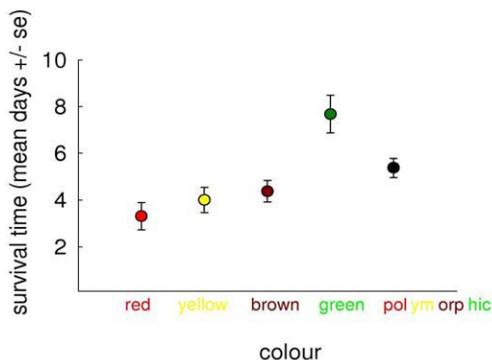
Figure 6. Comparisons of estimated mean survival times and associated standard errors for red, yellow, brown, or green monomorphic populations and for polymorphic (mix of all four colours) populations of artificial prey subjects exposed to predation by free-ranging avian predators. (For details, see Paper II.)

A significant effect of colour on survival time was evident also within polymorphic populations. I was able to tell which colour went extinct first in 21 out of 124 populations. Among the 21 replicates, the order of prey items that went extinct first was dependent on coloration, with red prey most frequently going extinct first, followed by yellow and brown (in no case did green prey go extinct first) (Fig. 7a). Similarly, I was able to determine which

of the four colours remained last in 14 of the 124 polymorphic populations. The order of prey items that survived the longest was dependent on coloration, with green prey being the last left in the majority of cases (10/14) (Fig. 7b).
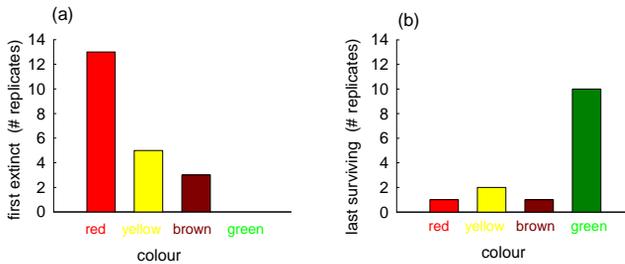

Figure 7. Comparison of distribution of prey colours that went extinct first (a) and those that survived the longest (b) within polymorphic groups of artificial pastry bait subjects exposed to predation by free-ranging avian predators. (For details, see Paper II.)

For individual pastry baits the estimated survival time was significantly dependent on the composition of the population. Red and yellow pastry baits survived longer when presented in polymorphic groups, compared to monomorphic, while the opposite was true for brown and green prey items that had a shorter mean survival time in polymorphic populations compared with monomorphic (Fig. 8, Paper II).

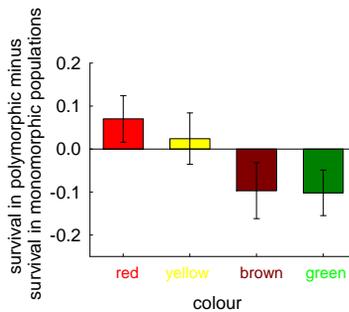*Figure 8. Consequences of belonging to a mono- or polymorphic prey population for prey of different colours. Figure shows the difference (mean +/- SE) between the mean percentage of artificial pastry prey subjects of four different colours presented in polymorphic and in monomorphic populations that survived for at least three days when exposed to predation by free-ranging avian predators. (For details, see Paper II.)*

No reduced predation risk in polymorphic prey populations

My conclusion from this experiment is that the colour of prey influences predation rate, but the prediction of a general protective effect of polymorphism was not supported in the study. At the individual level, there was a protective effect of being included in a polymorphic compared to a monomorphic group for two of the colours; red and yellow, while the opposite was true for green and brown prey items. For poorly protected colour morphs (like red and yellow in my study) it may thus be beneficial to belong to groups where better protected colour morphs (green and brown) are present. Hypothetically, such a protective effect may promote the initial evolution and spread of conspicuous warning signals (Paper II).

In natural colour polymorphic species the colour variants often co-vary with other traits, also behaviour (e.g., Forsman et al. 2002). An essential drawback of the artificial prey used in my experiment is that pastry baits do not behave. Co-variation of colour pattern with other traits (McKinnon and Pierotti 2010) and correlational selection may influence the relative susceptibility to predation (Forsman 1995, Forsman and Appelqvist 1998). Admittedly, this could mean that there is a protective effect of polymorphism in prey populations that I was not able to detect in this experiment. To test if co-adapted trait-value combinations enhance survival in polymorphic populations, it would be necessary to use natural prey populations.

From artificial pastry prey to real grasshoppers

Suggested protective effects of polymorphism in prey populations (search image, conservative choice of prey, and perceived density of prey populations) all refer to how predators perceive optional prey, not to interactions among the prey items themselves. Therefore, to compare predation risk in groups with different degree of colour variation (Paper II), the use of artificial pastry prey was useful, but at the same time meant that the pastry prey items did not behave, or, more correctly, all behaved in a fixed manner. If colour morphs represent co-variations of traits including behaviour (McKinnon and Pierotti 2010), then the effects of polymorphism may be enhanced (Forsman et al. 2008). To test the establishment capacity in groups with different degree of variation, where interactions among individuals may be important, I therefore used a natural model system, namely colour polymorphic pygmy grasshoppers (Paper III-IV).

Pygmy grasshoppers, *Tetrix subulata*, as a model system

The model system used in two experiments on establishment success and in long term observations under natural conditions, is the highly colour polymorphic *Tetrix subulata* (Orthoptera: Tetrigidae) pygmy grasshopper. *T. subulata* is a small (up to 15 mm), ground-dwelling, diurnal pygmy grasshopper species that is circumpolar and inhabits biomes ranging from tropical rainforests to arctic regions of Europe, Asia and North to South America (Mexico) except from south eastern United States (Rehn and Grant 1961, Holst 1986). *T. subulata* occupies open areas with access to open water or moist soil. They live on the soil surface and feed on algae, moss and dead partly decayed animal and plant matter in the litter. Nymphs develop through five (males) or six (females) instars before final moult (Holst 1986). Late instars and imagos hibernate and emerge in spring when mating season begins, in April-May in our study area in the south-east of Sweden. Females produce multiple egg pods, < 35 eggs/pod, but do not survive for more than one reproductive season (Holst 1986, Forsman 2001).

Colour morphs range from light grey via different shades of brown to black, with some morphs being uniform and others mottled or patterned with stripes or speckles (see cover photos). Colour morphs are genetically determined and seem not to be influenced to any important degree by developmental plasticity (Karlsson et al. 2009, Karlsson and Forsman 2010, Paper V). Importantly, pygmy grasshopper colour morphs represent integrated phenotypes (Forsman et al. 2008, McKinnon and Pierotti 2010) that co-vary with other ecologically important traits such as thermal physiology (Forsman 1999c, 2000), reproductive life-history (egg and clutch size, inter-clutch interval), body size (Forsman 1999a, Ahnesjö and Forsman 2003), predator avoidance behaviour, microhabitat utilization, and diet (Forsman 2000, Forsman et al. 2002, Ahnesjö and Forsman 2006, Karpestam and Forsman 2011).

The pygmy grasshopper *T. subulata* is wing dimorphic. In the same population both winged and wingless (or short-winged) individuals may occur (Nabours 1929, Rehn and Grant 1961). Only macropterous individuals with fully developed functional wings are capable of longer active flight (at least 75 meters) when experimentally released in unfavourable areas (Berggren et al. 2012). However, usually free-ranging, undisturbed *T. subulata* walk slowly on the ground or perform short jumps. Mark-recapture data indicate that they are sedentary and usually move only a few meters per day (Forsman and Appelqvist 1999, Caesar et al. 2007, Berggren et al. 2012).

Is establishment success higher in more variable founder groups under controlled conditions? (Paper III)

One of the predicted consequences of within population variation presented above (Forsman et al. 2008, Hughes et al. 2008, Paper I) is a higher establishment success in more variable founder groups. Forsman et al. (2008) argue that if morphs represent different combinations of ecologically important traits, then the morphs may have slightly different preferences for micro-habitat use and/or behave differently. This may reduce intra-specific competition, increase the evolutionary potential, and promote establishment in novel habitats, because of the higher chance in more variable founder groups to include pre-adapted morphs (Forsman et al. 2008).

The prediction of enhanced establishment success in more diverse founder groups has very rarely been tested. Crawford and Whitney (2010) showed higher establishment in groups with higher degree of genetic variation of the herb *Arabidopsis thaliana* on trays in a greenhouse, and Gamfeldt et al. (2005) showed higher establishment success in more genetically variable groups of *Balanus improvisus* barnacle larvae in the laboratory. Both these studies compared groups with different degree of genotypic variation, but it was not confirmed that the genetic variation was associated with phenotypic attributes, which makes the mechanism behind enhanced establishment uncertain. I tested establishment success in groups with different degree of variation in functionally important traits, under controlled conditions in outdoor enclosures (Fig. 9, Paper III).

Figure 9: An experiment to test for effects of founder diversity on establishment success was performed using Tetrix subulata *pygmy grasshoppers under controlled, semi-natural conditions in 80 outdoor enclosures in Vassmolösa, in the south-east of Sweden. Photo: L Wennersten.*

In 2009, we collected *T. subulata* pygmy grasshoppers from the wild and constructed small founder groups (propagules) of 6 individuals, 4 females and 2 males, with different degree of colour variation (Fig. 10). In the most homogenous groups all individuals belonged to one single colour morph, with 11 different morphs used among the 22 different homogenous groups. The most heterogeneous groups instead represented six different colour morphs each. Between these two extremes we had propagules with two, three, four, or five colour morphs represented.
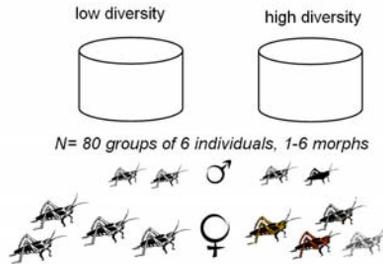

Figure 10: Establishment success was tested in Tetrix subulata *pygmy grasshoppers under semi-natural conditions in outdoor enclosures. Eighty founder groups with different degree of colour morph diversity (1-6 colour morphs) were used in the experiment. Each group consisted of four females and two males.*

In total, we collected individuals from five natural wild populations. To control for differences between populations, we never mixed individuals from different sources in any propagule. Mixing of individuals from different populations may cause unexpected advantages (hybrid vigour (Ebert et al. 2002)) or disadvantages (out breeding (Hufford and Mazer 2003)). The founder groups were introduced to their new environments in the enclosures (Fig. 9) in springtime when reproductive season begins in our study area in the south-east of Sweden. We used 80 outdoor enclosures (Paper III). One year after introduction to the new site, in spring 2010, we returned and counted the number of individuals using a standardized searching method. Each enclosure was searched by two persons for at least 5 minutes, and another 5 minutes after the last grasshopper was found. Each individual was caught and classified by sex, age (nymph or adult) and colour morph. All morph classifications were made by the same person (LW) to avoid inter-individual discrepancies. Since *T. subulata* pygmy grasshoppers live for one reproductive season only, the individuals counted the following year were offspring to the original founders. We used the number of individuals found in each enclosure as a measurement of establishment success.

Higher establishment success in more diverse founder groups in outdoor enclosures

After one year the number of grasshoppers was higher in those enclosures where more diverse founder groups had been released (Fig. 11, Paper III). Morph diversity after one year in the established populations in the outdoor enclosures was not associated with diversity in the founder groups. From one year to the next some of the colour morphs increased (e.g., speckled brown) while others decreased (e.g., black). This evolutionary change is probably a response to the selection regime. Many of the natural predators of *T. subulata* (birds, lizards, frogs, small mammals etc.) are excluded from the enclosures. Additionally, the sandy habitat where the enclosures were situated is not a typical habitat for *T. subulata* in the wild.
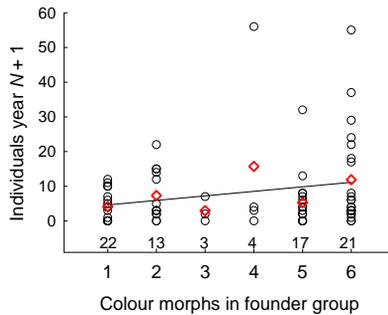

Figure 11: Number of Tetrix subulata *individuals present in outdoor enclosures after one year as a function of number of colour morphs included in founding propagules released the previous year. Data for 80 founding groups, each consisting of 6 (4 females and 2 males) individuals. Numbers above horizontal axis indicate sample sizes (i.e., number of replicates). Diamonds indicate means. (For details, see Paper III.)*

Is establishment success higher in more variable founder groups in the wild? (Paper IV)

To evaluate if the result of higher establishment in more variable groups under semi-natural conditions was repeatable also under natural conditions, across habitats, weather conditions and more complex selection regimes, we repeated the experiment on establishment in the wild during three subsequent years and released 61 experimental founder groups to different sites in the south-east of Sweden (Fig. 12, Paper IV).

Figure 12: An experiment to test for effects of founder group diversity on establishment success in the wild was performed using groups of Tetrix subulata *pygmy grasshoppers with different degree of diversity introduced to 61 experimental sites. Photo (L. Wennersten) from one of the experimental sites on the Baltic coast south of Kalmar, Sweden.*

We used small founder groups that consisted of seven (in 2007) or six (in 2008 and 2009) individual pygmy grasshoppers, four females and two (or three in 2007) males in each. The animals originated from four natural source populations in the wild, but individuals from different sources were never mixed in any propagule. In springtime in 2007, 2008 and 2009 the propagules were randomly assigned to one of the experimental sites. Prior to release, two persons carefully searched each potential release site under sunny conditions and with a temperature of at least 15°C, to confirm it was not already colonized by *T. subulata*. If no *T. subulata* were found, a randomly assigned founder group was released to the site. One year after introduction, we re-visited the experimental sites to look for offspring to the founders. Two persons searched each site for 10 minutes. All individuals that we found were captured and classified by sex, age (nymph or adult) and colour morph. All morph classifications were made by the same person (LW) to avoid inter-individual discrepancies. We used the number of individuals found at each site the subsequent year as a measurement of establishment success.

Higher establishment success in more diverse founder groups in the wild

We found an average of 5.8 (range 0-42) individuals per experimental site in the wild after one year. In congruence with the result from the controlled experiment in enclosures, the number of grasshoppers in experimental sites increased with increasing colour morph diversity in the founder groups (Fig. 13a, Paper IV). Moreover, relative colour morph diversity in the experimentally established populations in the wild increased with increasing number of colour morphs included in the founder groups (Fig. 13b, Paper IV). This last finding indicates that the positive effect of founder diversity on establishment may carry over across generations and influence also more long-term persistence.
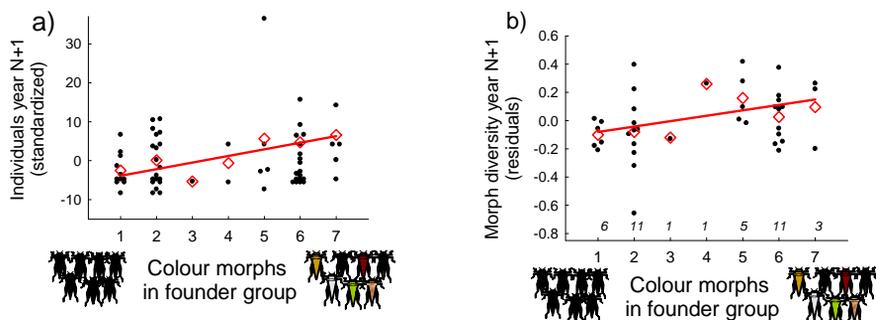
Figure 13. (a) Number of Tetrix subulata *pygmy grasshopper individuals captured at experimental introduction sites as a function of number of colour morphs included in founder groups released the previous year. Figure shows pooled data for three years, and values are standardized by year. (b) Colour morph diversity in experimental populations as a function of number of colour morphs included in the founder group. Colour morph diversity is expressed as residuals from year specific least squares linear regression of log number of colour morphs on log number of individuals. Red diamonds indicate mean values. Numbers in italics above horizontal axes indicate sample sizes. Overlapping data points are jittered in the x-axis direction. (For details, see Paper IV.)*

Conclusions from the establishment experiments (Paper III and IV)

The higher establishment success in more variable founder groups, both under semi-natural conditions in outdoor enclosures (Paper III) and in the wild (Paper IV), suggests a strong positive effect of within-group variation on establishment. These results are in accordance with expectations from theory (Forsman et al. 2008, Hughes et al. 2008, Bolnick et al. 2011, Paper I), and in agreement with previous studies that report on higher establishment success and increased population persistence in genetically more variable founder groups (Gamfeldt et al. 2005, Agashe 2009, Crawford and Whitney 2010). However, in comparison to these previous studies, the experiments reported here (Paper III and IV) were performed under more natural conditions and investigated the impact of diversity in functionally important traits.

In the wild (Fig. 13b), but not in the enclosures, morph diversity in the offspring generation was significantly associated with diversity in the founder groups. The different outcome in the enclosures and in the wild may be due to selection regimes. Since the enclosures were placed adjacent to each other and exposed to the same precipitation and other weather conditions and were free from avian predators, I expect selection stemming from environmental conditions to be similar in all replicates. In the field experiment, on the other hand, I expect selection regimes to differ more among years and among replicates due to differences in habitats, weather

conditions, and predation pressures. Some particular morphs may have been favoured by selection in the enclosures. The increase of some morphs (e. g., speckled brown) and decrease of others (e.g., black) points in this direction. In the wild, selection regimes are more complex (e.g., diversity in micro-habitats and predation) and the spatiotemporal heterogeneity may maintain phenotypic variation (Levins 1968, Hedrick 1986). Probably, no particular morph is superior across habitats and years and in heterogeneous environments individuals may actively choose different micro-habitats according to their phenotype (Edelaar et al. 2008, Karpestam et al. 2012b, Wennersten et al. 2012).

Suggested mechanisms for higher establishment success in more variable groups

I suggest three possible mechanisms for the higher establishment success in more variable founder groups;

i) The sampling effect (Fig. 5), that is, a higher probability in more diverse groups to include pre-adapted morphs suitable for the new conditions. This explanation is particularly relevant when morphs, as in *T. subulata,* represent trait-value combinations with different specializations for resource use and behaviours. However, since different colour morphs were used among monomorphic groups, a sampling effect should result in a high variance among the groups. Monomorphic groups with all individuals representing a well suited morph should be very successful, while the opposite should be true for monomorphic groups of morphs adapted for other conditions. This expectation was not met in the result from the enclosures; variance in number of offspring was not higher in monomorphic compared to polymorphic groups, if anything, the observed pattern was in the opposite direction (Fig. 11, Paper III). The result from the field experiment was similar to the enclosures; variance in number of offspring was not higher in monomorphic groups (Fig. 13a).

ii) According to niche complementarity, facilitation or social heterosis (Reusch et al. 2005, Nonacs and Kapheim 2007, Hughes et al. 2008, Nonacs and Kapheim 2008, Agashe 2009, Bolnick et al. 2011, Fig. 5) diversity is beneficial for the group, due to reduced competition among individuals (Forsman et al. 2008), reduced predation in more variable groups, or mutualistic interactions among individuals. However, since the experiments were not designed to test for an effect of complementarity, I am not able to conclude with certainty that niche complementarity contributed to higher establishment success in the enclosures or in the wild. To differentiate between these alternative hypotheses each morph has to be included both in monomorphic and polymorphic groups, and its performance compared between pure and mixed treatments (Reusch et al. 2005).

iii) A higher number of alternatives could explain a higher establishment success due to an evolutionary rescue effect (Bell and Gonzalez 2009). In sexually reproducing species recombination during meiosis gives rise to new combinations of alleles and thus a higher number of variants in the offspring generation in more variable founder groups for selection to act upon (Smith 1989, Agashe 2009).

Higher establishment success in more diverse groups, but what about adaptation?

Above, I have reported on a higher establishment success in more variable groups of *T. subulata* pygmy grasshoppers. Some of the quite small founder groups of 6-7 individuals managed to survive and reproduce, not only in outdoor enclosures (Paper III), but also in the wild (Paper IV). May this capacity to establish in new sites be associated with enhanced evolvability in this highly polymorphic species? Since colour morphs are genetically determined (Karlsson et al. 2009, Karlsson and Forsman 2010) and morph frequencies differ between generations (Paper III), established populations have undergone an evolutionary change. A more diverse founder group include a higher degree of standing genetic variation and may therefore have a higher capacity for adaptive changes (Bell and Gonzalez 2009). The results from the next study (Paper V), where I report on evolutionary response to changing environments in *T. subulata*, suggest that this may be the case.

Rapid evolutionary responses in replicated polymorphic populations (Paper V)

For polymorphic populations, it has been argued that both the capacity to withstand changed conditions, or to undergo adaptive evolutionary changes, should be enhanced in more diverse groups (Forsman et al. 2008, Hughes et al. 2008). Even if it has been known since Darwin (1859) that within population variation is a pre-requisite for adaptive evolution, it has often been regarded as a slow process. The most well known example of contemporary evolution is in *Biston betularia* Peppered moth where the melanistic (black) morph, unknown before 1848, almost replaced the paler form in fifty years during the industrial revolution (Kettlewell 1955, Grant et al. 1995), later decreased following the creation of smokeless zones from the middle 1950:s. In thirty years the frequency of the melanistic morph dropped from 94.2% in 1960 to 18.7% in 1994 (Grant et al. 1995).

Our highly polymorphic model system of *T. subulata* pygmy grasshoppers provides an ideal opportunity to test for micro-evolutionary responses to spatiotemporal environmental changes induced by forest fires. In fire ravaged areas, *T. subulata* populations sometimes increase substantially and then decline again some years after the fire event, along with the vegetation succession. We collected *T. subulata* (*n* = 5058) from 20 natural populations during the years 1995-2009 and compared the frequency of melanistic (black or very dark) individuals in burnt (*n* = 9 areas) and non-burnt (*n* = 11) areas. Burnt areas were visited one to four years after the fire event. Four of the nine burnt areas were visited in subsequent years to follow changes in morph frequencies. We found that in these burnt areas, the frequency of black individuals was very high, compared to populations in non-burnt areas (Fig. 14). Within burnt areas, the frequency of black individuals declined with time elapsed after the fire, coincidental with the vegetation succession in the following years (Fig. 14). The rapid response to environmental change could, theoretically, be explained by three different mechanisms; plasticity, biased immigration or evolutionary response to selection.
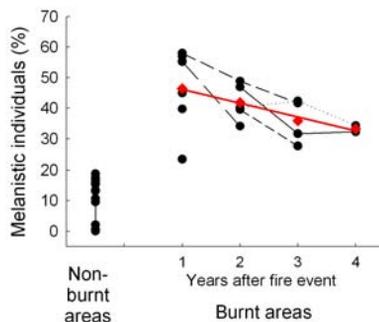

Figure 14. The incidence of black pygmy grasshoppers is higher in burnt than in non-burnt areas. Figure shows mean percentage of individuals that are melanistic for 11 populations in non-burnt areas and for 9 populations in burnt areas sampled at different times after the fire event. Black dots connected with lines indicate samples from successive years in the same population. Red squares represent mean values across populations within each year category, red line denotes fitted linear regression of yearly means. (For details, see Paper V.)

Plasticity does not explain higher frequency of melanistic individuals in burnt areas

To test the influence of plasticity on the high frequency of melanistic individuals, we reared 2070 individuals in a common garden experiment using offspring produced by wild-caught mothers, representing populations from burnt (*n* = 163 families) and non-burnt areas (*n* = 104 families). We found a higher frequency of melanistic offspring from burnt (mean percentage of

melanistic individuals across 163 families = 27%, range 0-100%) than from non-burnt areas (mean percentage of melanistic individuals across 104 families = 3.3%, range 0-66%, Paper V). Moreover, at the population level we found a strong association across populations between the frequency of melanistic individuals in captive reared offspring generation and wild caught parental generation in corresponding populations (Fig. 15, Paper V). This experiment suggests that colour morphs are genetically determined and not induced by plasticity. The result is in accordance with previous studies that report no impact, neither from rearing substrate (charcoal or white gravel) (Karlsson et al. 2009) nor from rearing density (Karlsson and Forsman 2010), or rearing temperatures (Forsman 2011) on morph frequencies. Even if we are not able to conclude with certainty that there is no environmental influence on morph frequencies whatsoever, these experiments strongly suggest a strong genetic determination of colour morphs. The higher frequency of black grasshoppers in burnt compared to non-burnt environments is therefore either a biased immigration of darker individuals into burnt areas, or a selective advantage for dark morphs in fire ravaged environments.
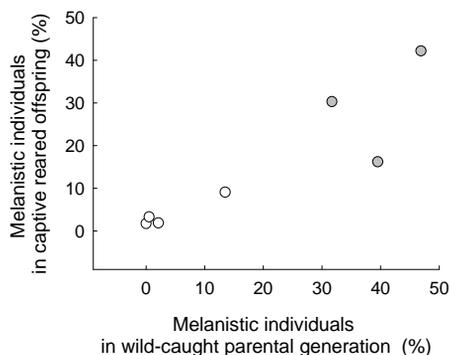

Figure 15. The incidence of melanistic individuals among offspring from different populations reared in a common environment is associated with that in the parental generation. Data for captive born individuals originating from different populations reared in a common environment from the time of hatching until maturity and for wild-caught individuals from the same populations. Data for wild-caught individuals include all males and females in the sample, not only the parents of the captive reared animals. Data for populations in burnt (grey filled symbols) and non-burnt (open symbols) environments. (For details see Paper V).

Biased immigration does not explain higher frequency of melanistic individuals in burnt areas

As already mentioned, *T. subulata* is polymorphic not only in colour patterns, but also in wing-length. Only individuals with fully developed functional wings are capable of longer active flights (Berggren et al. 2012). Thus, a

higher frequency of melanistic individuals in recently burnt areas could theoretically be explained by a higher immigration of black individuals, but only if either the black morph shows a higher proportion of long-winged individuals than lighter morphs, or if long-winged black individuals are more attracted by recently burnt areas.

To evaluate if a biased immigration could explain the high frequency of the melanistic morph, we compared the frequency of long-winged, potential long-distance migrants, between melanistic and non-melanistic individuals in a newly colonized, burnt area in 2009. A large natural fire (ca 125 ha) ravaged a coniferous forest in Påryd in the south-east of Sweden in July 2009. When we visited the site two months later, we only observed two individual *T. subulata* pygmy grasshoppers (one grey and one brown female). Next spring, 10 months after the fire event, we revisited the area and collected 85 adult *T. subulata* and classified them by sex, wing-length and colour morph. There was no significant difference in frequency of long winged individuals between melanistic (around 60%, *n* = 33) and non-melanistic (around 55%, *n* = 52) colour morphs (Paper V). This result indicates that a biased immigration is not a probable explanation for higher frequencies of melanistic individuals into burnt areas.

Selective benefits of melanistic coloration in burnt areas

Neither plasticity nor biased immigration are probable explanatory factors for the high frequency of melanistic individuals in fire ravaged areas, and we instead suggest that evolutionary change due to fluctuating selection regimes may explain both the initial rapid increase and the subsequent decline in melanism frequency in burnt areas (Paper V). Selection in fire ravaged environments may favour melanistic grasshoppers in different ways. First, dark individuals are likely to be better camouflaged against the blackened background that characterizes burnt areas (Karpestam et al. 2012a). Selection imposed by visually oriented predators, mainly birds, may therefore favour darker individuals. The decline of melanistic animals along with vegetation succession in subsequent years, when the environment becomes more heterogeneous, could be explained by a reduced beneficial effect of crypsis for dark individuals. Differences in relative crypsis among colour morphs against different backgrounds have previously been demonstrated in *T. japonica* pygmy grasshoppers (Tsurui et al. 2010). In *T. subulata* colour patterns have been demonstrated to influence predation rate and survival in free ranging individuals (Forsman and Appelqvist 1999), and under controlled conditions (Forsman and Appelqvist 1998, Civantos et al. 2004, Karpestam et al. 2012a). Second, colour morphs in *T. subulata* represent co-variation of traits, and it has been demonstrated that selection may act on other traits than coloration *per se* (Forsman and Appelqvist 1998). Surface temperatures in areas that have been blackened by fire can be very high (Ahnesjö and Forsman 2006) and it

has been shown that darker morphs prefer higher body temperatures, compared to paler morphs (Forsman 2000, Forsman et al. 2002).

Because of these potential benefits from crypsis and heat adaptations for darker individuals in burnt areas, we conclude that the changes in frequencies of black individuals represent remarkably rapid adaptive responses to the dark background in fire ravaged areas (Paper V). The co-occurrence of multiple morphs, representing genetic and phenotypic diversity, is most certainly a requirement for this rapid evolutionary response to fluctuating selection regimes due to evolutionary rescue (Bell and Gonzalez 2009), or recombination (Barton and Charlesworth 1998, Agashe 2009).

Review of empirical studies (Paper VI)

I reviewed experimental and comparative published studies on five of the twelve predictions from Paper I, namely; the predictions on vulnerability, fluctuations, extinction, distribution, and establishment. These five predictions were chosen because of their high importance for population persistence in a world characterized by rapid environmental changes.

In total I found 29 empirical studies, that met the stringent criteria of firm empirical testing for causality in groups with different degree of variation, or comparative analyses where related taxa with higher or lower degree of variation were compared (Paper VI). Twenty experimental studies compared outcome in manipulated groups where different number of clones, strains or morphs were included. Nine studies compared related taxa that differed with regard to diversity, most often species with or without variable coloration, but in one case the comparison was made between species with or without resource polyphenism (Pfennig and McGee 2010).

My review uncovered some strong taxonomic biases. Experimental studies included work on animals (n = 10, nine on invertebrates such as insects, crustaceans, amphipods and barnacles, and one on frogs), plants (n = 9), and bacteria (n = 1). Twelve of these twenty experimental studies were performed under laboratory, greenhouse, common garden or semi-natural conditions, the remaining eight experiments were carried out under more natural field conditions. In contrast to the experiments, most (8 of 9) of the comparative analyses examined vertebrates, such as birds (n = 3), reptiles (n = 3), fishes and amphibians (n = 1) and frogs (n = 1), and only one of the comparative studies included in this review was carried out on insects. None of the 29 experimental or comparative studies was performed on mammals.

The review revealed very strong support for the suggested predictions. In 28 of the 29 studies results were in accordance with predictions; more variable groups are reported to have reduced vulnerability to environmental

changes, reduced population fluctuations, reduced extinction risks, increased distribution range sizes and higher colonization or establishment success, compared to less variable groups. I found one study only (Vilas et al. 2006) that did not support the predicted reduced extinction risk in more variable populations, and no study that reported results in conflict with predictions. However, in all reviews aiming at interpreting combined results from different published studies, there is a risk of a bias from a higher proportion of studies with positively significant results to be published, called the file drawer effect. To evaluate this risk, I performed a file drawer analysis, following recommendations by Hunter and Scmidt (2004) and Rosenthal (1991). The result of this analysis indicates a high robustness for four of the five predictions. For the fifth prediction, reduced fluctuations in more variable populations, the low number of reviewed studies ($n = 3$) indicates that a file drawer bias can not be ignored (Paper VI).

Not all studies reviewed in Paper VI identified the mechanism(s) that mediated the positive effect of diversity. However, in *Zostera marina* sea grass, the reduced vulnerability to temperature stress in more variable populations was attributed to niche complementarity, rather than to a sampling effect, based on a comparison of relative performances of genetic alternatives in mono- and poly-cultures (Reusch et al. 2005). On the other hand, a selection effect is suggested to contribute to the higher population size and stability in more variable populations of *Tribolum castaneum* flour beetles in the ancestral resource treatment (wheat) due to higher fitness in one of the included strains (Agashe 2009). Presumably, the mechanisms that contribute to increased ecological success and performance of groups with greater phenotypic and genetic variability are not mutually exclusive, and multiple factors may be simultaneously involved (e.g., Crawford and Whitney 2010).

Implications and conclusions

The review of predicted consequences of within population variation revealed a general agreement on predictions, and a strong support from empirical studies, on higher establishment success, decreased vulnerability to environmental changes and higher evolvability in more diverse groups (Paper I and VI).

A higher establishment success in more diverse founder groups has been demonstrated here (Paper III and IV) and in previous studies (Gamfeldt et al. 2005, Crawford and Whitney 2010). Taking within group variation into consideration may therefore enhance the success of conservation biology projects, for instance in re-introductions of locally extinct populations or in re-stocking of declining populations. Higher establishment success is closely related to invasive capacity in populations and species. In this context, it is

interesting that some of the most well known invasive species (e.g., the Harlequin ladybird *Harmonia axyridis,* the Zebra mussel *Dreissena polymorpha,* the Spanish slug *Arion vulgaris,* and the lizard *Anolis sagrei*) are characterized by high levels of intra-specific (colour pattern) variation (Johnson and Carlton 1996, Kolbe et al. 2004, Majerus et al. 2006, Paper IV). Information on within species variation may therefore help to identify invasive species before they become invasive.

The predictions of reduced vulnerability to environmental changes and higher evolvability in more diverse groups (Paper I), are closely related. Even if the rapid evolutionary change reported on in Paper V is not compared in groups with different degree of diversity, I argue that it strongly illustrates the high importance of preserved within population diversity for sustainable populations in a world currently characterized by rapid environmental changes.

Other consequences of within population variation reported on in Paper I; broader niches, reduced intra-specific competition, and higher productivity in more variable groups, have not been tested in experiments reported on in this thesis, or reviewed from other studies in Paper VI, but a range of suggestions for further investigations are available in Paper I. For instance, the predicted higher productivity in more diverse groups is of high importance for increased but sustainable food production (Naeem et al. 2009).

The strong support for theoretical predictions reported on in Paper VI, further implicate the importance of population-level consequences of variation in conservation biology projects. However, Paper VI also revealed a bias in studied organisms with small, short-lived invertebrate species or plants used in the experiments, and larger, longer-lived vertebrate species (mammals excluded) in the comparative analyses, highlighting the importance of a broad approach in future research projects aiming to evaluate the generality of the findings.

Why are not all populations variable?

If there are so many advantages from within population variation (Table 1 and Paper I), why then are not all populations phenotypically variable? I have already emphasised that my thesis does not consider evolution or maintenance of polymorphism, although some words on these issues may be needed to explain why polymorphism is not more common.

First, my thesis mainly concerns colour polymorphism, something that may be more widespread than we think (McKinnon and Pierotti 2010), but colour polymorphism is just one aspect of intra population variation. There are also other aspects of phenotypic variation within populations, including variation stemming from polymorphism in other traits than colour pattern, plasticity, or randomized switches. Additionally, there is genetic

polymorphism, stored in the genome of individuals, but not expressed in phenotypes and thus not available for selection to act upon. Such standing genetic variation is still crucial for evolutionary rescue.

Second, if one specific morph in a variable population is superior over a range of conditions, this morph will out-compete the others and the population will transform from poly- to monomorphism. Transitions in this direction are probably common because if they were rare, the same polymorphism should be present in different, related taxa, and this does not seem to be the case (Forsman et al. 2008). Even if populations may benefit from within-group diversity, selection at the level of individuals may still favour specific trait values and promote the evolution of monomorphism.

Third, selection acts on fitness consequences of phenotypes among individuals within groups, and on fitness consequences of variation at the population-level among populations (Sober and Wilson 1998, Okasha 2006). The transition from phenotypic mono- to polymorphism may evolve by mutations, gene flow, selection, or introgression (Forsman et al. 2008), but evolution of traits of individuals will never occur due to enhanced future fitness prospects at the population-level. This means that even if there are substantial benefits of within-population variation, this is not enough for intra population diversity to evolve.

Fourth, diversity may not always be beneficial for populations, as discussed below.

Is diversity always beneficial for populations?

In theory, a population at evolutionary equilibrium in which all individuals are perfectly adapted may suffer a reduction in average fitness (i.e., genetic load (Lande and Shannon 1996)) due to the addition of inferior genotypes as a consequence of mutation, segregation, and substitution by selection (e.g., Haldane 1957, Maynard Smith 1976, Crow 1993). Mal-adapted individuals with reduced fitness may survive and reproduce only when included in a diverse population that includes better adapted individuals. The longer surviving time for poorly protected prey items when included in polymorphic prey populations reported in Paper II may serve as an illustration of this phenomenon. Gene flow may not only introduce new alternative alleles, but also constrain local adaptation in the wild (Nosil 2009). In adjacent populations where different selection regimes (different host plants) have resulted in separate local adaptations, it has been shown that migration from one population to the other results in migration load, that is, a reduced fitness at the population level due to mismatch between phenotypes and habitat (Bolnick and Nosil 2007). However, the role of genetic variation for adaptive evolutionary response to rapidly changing conditions, is beyond controversy

(Fisher 1999). Therefore, within-population diversity is crucial for protection of biodiversity at higher levels, for species and ecosystems (Bradshaw 1991).

Summary

In my thesis I report from reviews, empirical tests, and long term observations that:

A. Higher within population variation is predicted to result in broader resource use, reduced intraspecific competition, reduced vulnerability to environmental changes, more stable population dynamics, higher colonization and establishment success, higher invasive potential, larger distribution ranges, higher evolvability, higher productivity and population growth rate, reduced extinction risk, and higher speciation rate. In most cases, the predictions are similar regardless of source of variation (Paper I).

B. Polymorphism may not generally protect populations from predation, but for individual prey items, predation risk depends both on its own coloration and on the coloration of the other members of the same group, that is, if the group is mono- or polymorphic (Paper II).

C. Colour polymorphism enhances establishment success in small founder groups of pygmy grasshopper, both under controlled semi-natural conditions (Paper III) and in the wild (Paper IV).

D. Colour polymorphic populations of pygmy grasshoppers may adapt very rapidly to environmental changes (Paper V).

E. Predictions of ecological consequences of within population variation are generally supported by results of experiments and comparative analyses, but there are relatively few published studies and there is a bias in the organisms that have been used for experiments and comparative analyses, respectively (Paper VI).

Finally, I claim that an enhanced knowledge of the consequences of variation may increase our ability to understand the ecological dynamics of natural populations and communities, develop more informed management plans for protection and restoration of biodiversity, suggest possible routes to increased productivity in natural and managed biological systems, and resolve inconsistencies in patterns and results seen in studies of different model systems.

Future perspectives

Many of the theoretical predictions presented in Paper I still remain to be tested. In particular, consequences from variation stemming from plasticity or randomized switches have rarely been compared to homogenous populations, in other perspectives than the adaptive value of the plastic response in itself (Paper VI).

Some areas that need future investigations to provide important novel insights are:

- compare vulnerability to environmental changes in groups with different degree of diversity. Repeat the test in different model systems and compare the outcomes with diversity stemming from genetic polymorphism, developmental plasticity and randomized switches,
- compare performances (e.g., predation rate, establishment success, evolvability) in groups with different degree of diversity stemming from developmental plasticity,
- use comparative analyses to compare niche breath, fluctuation in population dynamics, invasiveness, distributional range size and extinction risk in related, variable and non-variable taxa,
- perform experiments on fluctuation in population dynamics, establishment, and extinction risk, and compare the outcomes when experiments are performed in the field with laboratory controlled conditions,
- evaluate ecological effects of diversity in groups of organisms poorly studied so far (e.g., bacteria, mammals, vertebrate taxa in experiments, and invertebrates in comparative analyses),
- design experiments in a way that enable evaluations of possible mechanisms contributing to the outcome, (e.g., sampling effect, complementarity, or evolutionary rescue).

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