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Invasive Species: Genetics, Characteristics and Trait Variation Along a Latitudinal Gradient

Thesis for the degree of Philosophiae Doctor

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Norwegian University of Science and Technology
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Declaration of contribution

I JHa, KPA, and BJG designed the study. KPA, JB, OC, SAOC, PAD, MD, PDF, MH, AJ, IL, AK, JP, and ZAR collected samples. JHü did the molecular analysis. JHa wrote the manuscript with inputs from all co-authors.

II Shared first authorship between EE and KPA. KPA and BJG designed the study. KPA, PAD, and ZAR collected samples in the wild. KPA set up the experiment. EE did the measurements in the greenhouse and wrote the manuscript with help from KPA. JT, Christophe Pelabon (CP) and EE did statistical analysis. CP also contributed to the writing of the manuscript. However, due to later disagreement between CP and EE, CP has retracted from authorship of this manuscript. All co-authors commented on the manuscript.

III KPA, BJG and CP designed the study. KPA, PDF, JB, OC, SAOC, MD, MH, AK, IL, JP, KV collected samples. KPA set up the experiment and did all measurements. KPA and CP did statistical analysis. KPA wrote the manuscript with contribution from CP and BJG and all co-authors commented on the manuscript.

IV KPA and BJG designed the study. KPA, PDF, JB, OC, SAOC, MD, MH, AK, IL, JP, and KV found populations in different regions. KPA, SAOC, MD, AK, IL, and JP collected samples. KPA wrote the manuscript. CP gave advice for statistical analyses, discussed results, and commented on some early version of the manuscript. All co-authors commented on the manuscript.

GENERAL INTRODUCTION

> *"Nowadays we live in a very explosive world, and while we may not know where or when the next outburst will be, we might hope to find ways of stopping it or at any rate of damping down its force. The explosion mentioned here is none other than ecological explosions."*
>
> *CHARLES S. ELTON (1958)* in his book, The Ecology of Invasions by Plants and Animals

Biological invasion has become one of the serious threats to biodiversity (Glowka *et al.*, 1994, Vitousek *et al.*, 1996) and may pose threats to human health (Mazza *et al.*, 2014). With the increase in globalisation during the second half of the last century, the introduction of species beyond their native ranges has increased exponentially (Mack *et al.*, 2000, Essl *et al.*, 2011). These introductions are either deliberate for various production purposes or for their ornamental quality or accidental introductions of seeds or propagules (Keane and Crawley, 2002). Upon introduction, to be able to establish successfully, the introduced species has to pass through different barriers in the recipient environment. Those barriers include geographic barriers, environmental barriers, reproductive barriers, and dispersal barriers (Richardson *et al.*, 2000, Theoharides and Dukes, 2007). Even if they may be introduced into similar abiotic (e.g. climatic or edaphic) conditions as in their native ranges, the introduced species may at least face a new biotic environment (Williamson and Fitter, 1996). Not all introduced species are able to overcome those barriers and become invasive. Williamson & Fitter (1996) proposed the *"Tens rule"* on the basis of non-native British flora and fauna which suggests that 1 in 10 introduced species will escape and appear in the wild, 1 in 10 of those escaped will become naturalised and 1 in 10 of those naturalised will become invasive. Although the fraction of introduced species becoming invasive seems very small, the impact caused by them is considered as the second major threat to environment after habitat destruction (Glowka *et al.*, 1994). Overall, the invasion process is grouped into three major stages: **introduction**, **naturalisation**, and **invasion** (Richardson *et al.*, 2000, Theoharides and Dukes, 2007) with different barriers acting on each (Figure 1.).

Introduction is the arrival of propagules beyond their native range by means of different vectors. Introduced species may or may not be able to survive and colonise in the introduced area. However, there is likely to be a higher chance of survival and colonisation if high numbers of propagules are transported (Kolar and Lodge, 2001). Survival and colonisation depend on a number of abiotic and biotic factors in the novel environment (Sakai *et al.*, 2001). Colonisation events may involve genetic bottlenecks as the number of initial colonists is often very small. Thus the amount of genetic variance in founding populations will be lower than the amount of genetic variation present in source populations (Nei *et al.*, 1975).

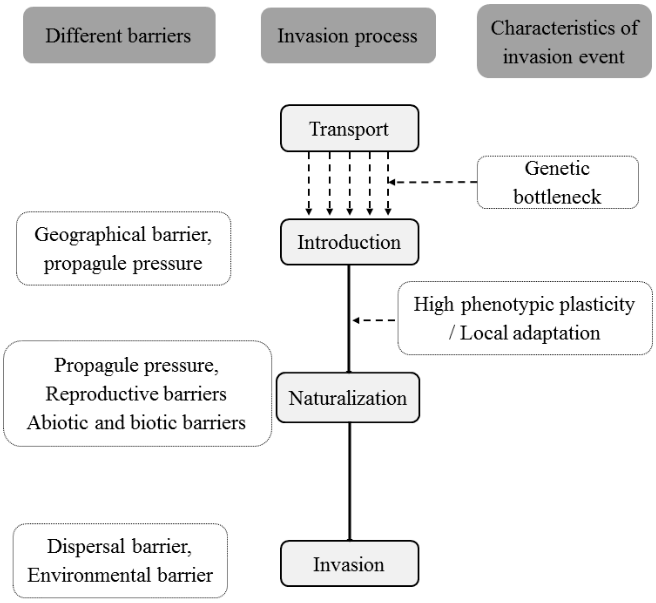

Figure 1. Diagrammatic sketch of an invasion process with different barriers and characteristics in each step. Modified from Richardson et al.(2000) and Theoharides & Dukes (2007).

After successful establishment, the species may be naturalised if it overcomes the environmental and reproductive barriers in the introduced range. Before widely spreading into the invaded surrounding environment the introduced species passes through the **lag phase** which may correspond to a lack of genetic variation (Sakai *et al.*, 2001). In invasive species this phase is generally considered a preparation phase for adaptive evolution. Multiple introductions from source populations, migration and gene flow between populations in the invaded environment may decrease the time of a lag phase, leading to rapid adaptive evolution (Kawecki and Ebert, 2004). Once naturalised, the local spread of invasive species depends on many factors including propagule pressure, dispersal mode, vital rates etc.

For successful management of invasive species and to prevent such invasions, understanding mechanisms underlying biological invasions are needed. Since Charles S. Elton's (1958) pioneering book on invasion ecology, *The Ecology of Invasions by Animals and Plants*, many studies have tried to find possible mechanisms behind the success of invasive species. A plethora of mechanisms are proposed for the success of invasive species (see Hierro *et al.*, 2005, Daneshgar and Jose, 2009 for review). Of them, research has focused on three main themes: a) pre-adaptation – the characteristics that promote invasiveness such as high competitiveness, reproductive output and phenotypic plasticity are already present in the native range (Lee and Gelembiuk, 2008, Mason *et al.*, 2008, Hejda *et al.*, 2009, Schlaepfer *et al.*, 2010); b) evolution of high phenotypic plasticity after introduction – allows introduced populations to rapidly cope with novel environmental conditions (Richards *et al.*, 2006, Caño *et al.*, 2008, Davidson *et al.*, 2011); and c) rapid local adaptation – exotic populations evolve by adapting to local selective pressures (Maron *et al.*, 2004, Dlugosch and Parker, 2008, Colautti and Barrett, 2013). One way to study why some are invasive and some are not is to study the traits of the introduced species. Life-history traits that make species more invasive have been of continuing interest because of their potential predictive power on overall species performance (Violle *et al.*, 2007, Öckinger *et al.*, 2010). Furthermore, such information is desirable for explaining (and therefore predicting) invasions either under the current environmental conditions or under predicted future climates (Rejmánek and Richardson, 1996, Macel *et al.*, 2007, Pyšek and Richardson, 2007).

Biological invasion is a complex mechanism. It can therefore be necessary to study different aspects of invasion. This thesis focuses on three aspects of biological invasion: *genetics*, *characteristics* of invasive species, and *trait variation in native and invasive species* along a latitudinal gradient in a natural environment. To understand these aspects, I used three species of *Impatiens*: *Impatiens noli-tangere*, *I. parviflora* and *I. glandulifera*. The first one is native to Europe and the latter two are highly invasive species in Europe. To study genetics and characteristics (Paper **I, II**, and **III**), I used *I. glandulifera* and for the last study whether the invasive species respond stronger to nitrogen and temperature than the native species, I used *I. noli-tangere* and *I. parviflora* (Paper **IV**). Before explaining the fundamental issues, genetics and characteristics of invasive species, I first present some terminology used in invasion ecology because there are many terms used interchangeably often leading to confusion (Richardson *et al.*, 2000, Colautti and MacIsaac, 2004, Falk-Petersen *et al.*, 2006). Aliens, weeds, pest species, biological pollutants, non-native, invasive alien species, non-native invasive species are some of the commonly used interchangeable words and phrases to describe non-native species which occur in regions outside their native range (Richardson *et al.*, 2000, Colautti and MacIsaac, 2004). Box 1 contains the recommended terminology for invasion ecology (Richardson *et al.*, 2000).

Throughout this thesis, I used the terminology recommended by Richardson *et al.* (2000). In the following sections, I explain the genetics of invasive species, then the possible characters (pre-adaptation, phenotypic plasticity, local adaptation) of invasive species and then trait variation in native and invasive species along a latitudinal gradient. In the final section, I will describe my own research on these aspects.

Alien: the species is present outside its native range due to intentional or accidental introductions. The term may be interchangeable with exotic, non-native, non-indigenous.

Casual alien: an alien species that may flourish and even reproduce occasionally in an area, but does not form self-replacing populations and relies on repeated introductions for its persistence. The term is interchangeable with transients, occasional escapes, and adventive.

Naturalised: an alien species that sustains populations over year to year without human influence.

Invasive: naturalised plants that produce large numbers of offspring that can persist over longer distances from parents.

Weeds: plants not necessarily alien but growing in sites where they are not wanted and usually have detectable negative economic or environmental effects.

Native range: a region where a species naturally occurs.

Introduced or exotic range: a region where the species has spread to with the assistance of humans or other means when it would otherwise be restricted due to geographical barriers.

Box 1: Terminology used in invasion ecology. Adapted from Richardson et al. (2000).

Genetic diversity in invasive species

As briefly described above, populations of invasive species suffer from genetic bottlenecks after introduction because the number of initial colonists is often small (Nei *et al.*, 1975). Moreover, sequential bottlenecks during colonisation and introduction would further reduce genetic diversity (Barrett and Kohn, 1991, Clegg *et al.*, 2002, Estoup *et al.*, 2004). Thus, introduced populations are typically less genetically diverse than their source populations (Amsellem *et al.*, 2000, Estoup *et al.*, 2004, Dlugosch and Parker, 2008). This, along with high risk of inbreeding depression resulting from a population-level bottleneck, may limit the population growth (Allendorf and Lundquist, 2003) and the introduced species' ability to adapt to new environments (e.g. Kinziger *et al.*, 2011). In spite of this, many invasive species that have gone through population bottlenecks are successful, a phenomenon commonly referred to as the genetic paradox of invasive species (Allendorf and Lundquist, 2003, Frankham, 2005).

However, the loss in genetic diversity can be counteracted by different genetic events. For example, polyploidisation and hybridisation (Ellstrand and Schierenbeck, 2000) or multiple introductions from source populations or within invaded populations may generate a high level of genetic diversity in the introduced range (Novak and Mack, 1993, Maron *et al.*, 2004, Genton *et al.*, 2005, Dlugosch and Parker, 2008, Shirk *et al.*, 2014), sometimes even higher than in the native range (e.g. Kolbe *et al.*, 2004, Genton *et al.*, 2005). Multiple introductions can usually bring a large amount of genetic variation and generate novel genetic combinations. For example, increases in genetic diversity in invasive species have been reported in an invasive wetland species *Phalaris arundinacea* L. in North America (Lavergne and Molofsky, 2007); *Geranium carolinianum* in China (Shirk *et al.*, 2014) and *Ambrosia artemisifolia* in France (Genton *et al.*, 2005).

Studying genetic diversity has received much scientific interest, especially during the past 40 years to assess invasion history and for successful management of invasive species. Integrating genetics with biological invasion is crucial and can reveal characteristics that allow a species to become invasive (Lee, 2002) and to understand the introduction patterns, expansion and gene flow during biological invasion which is important for making sound management decisions (e.g. Rollins *et al.*, 2009).

Phenotypic plasticity

Phenotypic plasticity, a property of one genotype to produce different phenotypes in response to different environmental conditions (Bradshaw, 1965), has been suggested as an important characteristic that contributes to the success of invasive species in a novel environment (Baker, 1965, Richards *et al.*, 2006, Davidson *et al.*, 2011). The phenotypic variance of a trait is an outcome of genotypic variance, environmental variance and the interaction of both, and is generally expressed as:

$V_P = V_G + V_E + V_G \times V_E + V_{error}$

where:

V_P = total phenotypic variance of a trait

V_G = genetic variance

V_E = environmentally generated variance

$V_G \times V_E$ = genetic variance for phenotypic plasticity

V_{error} = unexplained variance

The most common way to visualise phenotypic plasticity is via the *reaction norm* (Figure 2). Very often, reaction norms and plasticity are used synonymously but they are not the same. Reaction norm is a function that describes the relationship between phenotype and environment whereas plasticity is a feature of the reaction norm (Figure 2) (Pigliucci, 2001). In other words, a genotype can be plastic or not plastic but will have a reaction norm in both conditions. Reaction norms are often simplified and appear as straight lines (Figure 2) as many of the green house experiments often use only two environmental factors (high vs low nutrients, light etc.) (DeWalt *et al.*, 2004, Caño *et al.*, 2008, Qing *et al.*, 2011). However, in reality they may be of very complex shapes (for example see non-linear reaction norms observed for most traits in paper **III**) (Hulme, 2008).

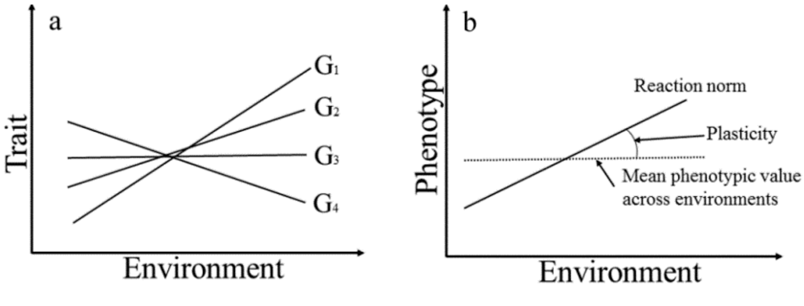

Figure 2: a) Illustration of phenotypic plasticity using reaction norms for four genotypes. Each line represents one genotype and its phenotypic expression along the environmental gradient, b) Relationship between plasticity and reaction norm.

Studies on phenotypic plasticity have largely focused on genotype-environment interactions (DeWitt and Scheiner, 2004) and linking phenotypic plasticity to invasive species is important for better understanding its role in the geographic distribution, successful colonisation and/or high abundance in the invasive range (Hulme, 2008). Higher plasticity of traits in invasive species than in their native congeners has been widely predicted to be a key trait for explaining why introduced species are so successful in their introduced environments (e.g. Schlichting and Levin, 1986, Daehler, 2003, Pyšek and Richardson, 2007, Funk, 2008) and is generally considered an important characteristic for success during colonisation events (Ghalambor *et al.*, 2007). Such plasticity characteristics in invasive species might already be present in the native range (pre-adaptation hypothesis) (Hejda *et al.*, 2009, Schlaepfer *et al.*, 2010) or may evolve after colonization (genetic-shift hypothesis) (DeWitt and Scheiner, 2004, Caño *et al.*, 2008, Qing *et al.*, 2011).

Local adaptation

Local adaptation is defined as the genetic differentiation resulting from adaptation to local environmental conditions (Kawecki and Ebert, 2004, Blanquart *et al.*, 2013). An adaptation is thus a feature of an organism that evolved in response to an identifiable form of natural selection. The concept of local adaptation parallels Lamarck's first law proposed in *Philosophie zoologique* in 1809 (Lamarck, 1809) which states that organisms acclimatize to their environment to improve performance. The pre-requisite for local adaptation is genotype × environmental interaction for fitness. Local adaptation may be constrained by a lack of genetic variation and hindered by gene flow (Kawecki and Ebert, 2004).

One way to measure local adaptation is reciprocal transplantation where the performance of a local population and a population originating from a different habitat are compared under similar environmental conditions giving "local" vs "foreign" condition (Leimu and Fischer, 2008): local adaptation means that in each habitat, the local population is expected to show higher fitness than the foreign population (Figure 3). However, such reciprocal transplantation experiments are often not suitable for invasive species because of ethical or legal reasons (Hulme, 2008). An alternative approach is greenhouse experiments where populations (genotypes) from different regions along latitudinal gradients are exposed to similar environmental conditions whilst controlling for other factors. If variation in morphological and phenological traits in the green house experiments are correlated to the environment of population origin and are conserved in subsequent generations, this is an indication of adaptive differentiation.

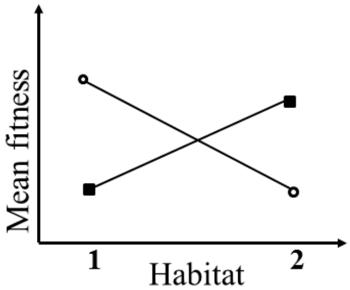

Figure 3: Hypothetical reaction norm of genotype × habitat interaction for fitness specifying the local vs. foreign criterion. Circles: genotypes originating from habitat 1; Squares: genotypes originating from habitat 2.

Loss of genetic diversity during introduction and subsequent range expansion might limit local adaptation possibilities in the introduced region (Lambrinos, 2004). However, evolutionary processes, such as genetic drift, migration, and/or multiple introduction events could form novel genotypes and increase standing genetic variation on which natural selection could act, leading to the evolution of locally adapted genotypes (Kolbe *et al.*, 2004, Shirk *et al.*, 2014). Indeed, several studies have shown that invasive species are often able to adapt very rapidly (e.g. Maron *et al.*, 2004, Montague *et al.*, 2008, Monty *et al.*, 2013) and expand their range (Colautti and Barrett, 2013).

Latitudinal gradient as a model

Latitudinal gradients are excellent natural laboratories to study plastic responses and/or adaptive differentiation in plants (Endler, 1977, Macel *et al.*, 2007). Latitudinal gradients generate large-scale environmental heterogeneity. For example, temperature, soil resources and duration of growing season decrease with increasing latitude (Reich and Oleksyn, 2004), whereas summer day length increases towards higher latitudes (Bradshaw and Holzapfel, 2008). Plants at different positions along these gradients face distinct growing conditions. Adaptation to local environmental conditions results in genetically based phenotypic differentiation (Kawecki and Ebert, 2004). Also, along latitudinal gradients populations are more scattered and gene flow between populations is likely to be low. Limited gene flow and increased inbreeding often lead to higher genetic differentiation (Kawecki and Ebert, 2004). Because of genetic differentiation, morphological and phenological traits of native plant populations show clinal variation to associated environmental variation along latitudinal gradients. If invasive populations show clinal variation parallel to that of native populations, it is suggested that adaptive evolution is occurring in the invasive species (e.g. Kollmann and Banuelos, 2004, Maron *et al.*, 2004, Colautti and Barrett, 2013).

Latitudinal gradients are also often used to study responses of species to global warming (De Frenne *et al.*, 2013). In general, temperature decreases with increasing latitude. Very often latitudinal gradients are used as a surrogate of temperature gradients to study the relative effect of temperature on the response of a species. However, in the natural environment multiple environmental factors vary which complicates unravelling the effect of a single environmental factor (Bradshaw and Holzapfel, 2008). Therefore, to describe the effect of temperature on trait variation, instead of using latitude as a surrogate, patterns of variation should be evaluated against temperature and covarying environmental variables (Körner, 2007, Graae *et al.*, 2012).

Use of traits in ecological research

Traits – any morphological, physiological or phenological features measurable at the individual level (Violle *et al.*, 2007) – are widely used in ecological and evolutionary studies ranging from individual to ecosystem levels (see Kattge *et al.*, 2011). A trait may influence the performance of an individual which in turn influences (directly or indirectly) the fitness of that individual. It reflects the response of a species to the abiotic and biotic environments (Valladares *et al.*, 2002). Therefore a focus on traits provides a quantitative estimation and promising prediction of the response of a species to environmental change

(McGill *et al.*, 2006, Westoby and Wright, 2006). I briefly present the functional role of some of the important traits in plants.

Plant height, an important morphological trait in plants, is strongly correlated with life span and time to maturity and is considered a surrogate of competitive ability (Moles *et al.*, 2009, Pérez-Harguindeguy *et al.*, 2013). Leaf area is linked to light availability and photosynthetic capacity, and is a good representative of soil resource availability and nutrient cycling (Vendramini *et al.*, 2002, Wright *et al.*, 2004). Above-ground biomass is an outcome of plant performance linked to plant fitness since above-ground biomass and seed production of annual species are often correlated (Thompson *et al.*, 1991, Shipley and Dion, 1992). Seed mass is a key ecological trait that is considered relevant for plant regeneration, including seedling survival rates and dispersal (Westoby, 1998, Leishman *et al.*, 2000), with smaller seeds dispersing farther away from the mother plant but with fewer stored resources, whereas larger seeds have shorter dispersal distances with higher stored resources (Pérez-Harguindeguy *et al.*, 2013). Number of seeds per capsule is an indication of pollination success and resources invested in reproduction which in turn is related to reproductive output.

In response to associated variation in environmental factors (see above) along latitudinal gradients, plant traits show clinal variations. For example, a review by Moles *et al.* (2009) found that plant height decreased with increasing latitude and the pattern was mainly driven by precipitation in the wettest months. Similarly, seed mass also decreased with increasing latitude (Moles and Westoby, 2003) In response to the shorter growing season towards higher latitudes, populations originating from northern latitudes start flowering earlier and at a shorter height (e.g. Li *et al.*, 1998, Maron *et al.*, 2004, Montague *et al.*, 2008).

AIMS

The aim of this study is to study the fundamental issues in invasion biology: genetics, characteristics of invasive species, and trait variation along a latitudinal gradient. A better understanding of these issues is important to help prediction and proper management of invasive species. To obtain information on these, we used three species of *Impatiens*: *Impatiens noli-tangere*, *I. parviflora*, and *I. glandulifera*. Specific objectives of this thesis are:

1. To study genetic diversity in the native and invasive populations of *Impatiens glandulifera* (Paper **I**).
2. To evaluate if *Impatiens glandulifera* is pre-adapted to high invasiveness with high phenotypic plasticity on growth and/or reproduction or if it has evolved such characteristics after introduction (Paper **II** and **III**).
3. To study whether the invasive *Impatiens parviflora* is more responsive to nitrogen and/or temperature than the native *I. noli-tangere* (Paper **IV**).

METHODS

Study species

Impatiens (Balsaminaceae) is a genus of over 1000 species of annual and perennial herbs mainly distributed across Asia and Africa (Clifton, 2000, Janssens *et al.*, 2006). In this thesis, I use three species of *Impatiens*: *Impatiens noli-tangere* L., *I. parviflora* DC., and *I. glandulifera* Royle (Figure 3). On the following pages, I briefly describe these three species.

Figure 4: Studied species of *Impatiens*: (a) *I. noli-tangere*, (b) *I. parviflora*, and (c) *I. glandulifera* in their natural environment (Photos: Kamal Prasad Acharya)

***Impatiens noli-tangere* L.**, touch-me-not balsam (Figure 4a), annual herb, about 20–180 cm tall, is native to Europe (Hatcher, 2003). It is widely distributed across the Northern temperate zones of Asia, Europe and North America (Hatcher, 2003). The species grows on damp to wet, often waterlogged soils, along riverbanks. *I. noli-tangere* frequently has very few associated species in the herb layer and forms pure stands. In central Europe, the species can emerge from late February onwards and remain until late November, producing flowers from early July to late August (Hatcher, 2003). The flowers are protandrous; after the anthers have fallen off, the stigma becomes receptive, preventing self-pollination (Masuda and Yahara, 1994). The plants are usually pollinated by Hymenoptera and Diptera (Hatcher, 2003). The species has no permanent seed bank (Markov, 1991). Mass-scale extinctions have sometimes been reported and it rarely reappears at sites from where it was lost (Tinchý, 1997).

***Impatiens parviflora* DC,** small flowered touch-me-not- balsam (Figure 4b), annual herb, about 20–150 cm tall is native to Central Asia (Coombe, 1956). It grows in moist and shady forests, riparian scrub and woodlands. It sometimes coexists with native *I. noli-tangere* (Lambdon *et al.*, 2008 and KP Acharya pers. obs.) and often grows on soil with high nitrogen content. The species is one of the highly invasive species is Europe (Lambdon *et al.*, 2008). It was first reported from Europe in 1831 from a botanical garden in Geneva (Jørgensen, 1926) and after a few decades escaped to adjoining regions. At present, the species is reported from most European countries (Lambdon *et al.*, 2008). The species is known to be highly plastic (Elemans, 2004). The species can emerge from late March to early April, and starts producing flowers from late May or early June until late September or early October (Coombe, 1956). The flowers are protandrous and usually pollinated by Coleoptera and Diptera.

Impatiens glandulifera Royle, Himalayan balsam (Figure 4c), one of the tallest annual herbs of about 3 m tall (Andrews *et al.*, 2005), is native to western Himalaya where it grows between 2000–4000 m a.s.l. (Polunin and Stainton, 1984, Beerling and Perrins, 1993). There is controversy about the introduction history of this species in Europe. It is widely cited that the species was first introduced from Kashmir to Kew Gardens, England as an ornamental plant in 1838 (Beerling and Perrins, 1993) and by 1982, it had spread all the way to northeast England (Valentine, 1978, Beerling and Perrins, 1993, Pyšek and Prach, 1995). But, *"Kreis ahrweiler heimatjahrbucharchiv"* available online (http://www.kreis-ahrweiler.de/kvar/VT/hjb2005/hjb2005.20.htm accessed on 01.07.2014) mentions that the species was found in the botanic garden of Dresden, Germany in 1832 and later introduced to England as an ornamental plant. The plant became naturalised in England by 1855. It further spread across Europe through deliberate introductions into botanic or private gardens or unintentional spread facilitated by transport along rivers (Pyšek and Prach, 1995). The species grows along riverbanks, in shaded habitats some distance from rivers or even along road-sides and around field borders (Pyšek and Prach, 1995). The plants produce protandrous flowers from July to October, setting seed from mid-July onwards (Valentine, 1978, Beerling and Perrins, 1993). Flower colour is highly variable from dark purple to pink and white. The species has a limited seed bank (Perrins *et al.*, 1993).

Several aspects of the invasion characteristics of *Impatiens* have been studied. Comparative studies on the above-mentioned species (one native and either of the two invasive species) were carried out to find why introduced *Impatiens* species are successful in their invaded habitats. Key findings of some of these studies are mentioned in the following section.

Genetic analysis of invasive *I. glandulifera* from its invaded environment shows evidence of multiple introductions of this species in Finland (Nagy and Korpelainen, 2014). Despite multiple introductions, genetic diversity in invasive populations was lower than in populations from native environments. As mentioned above, the species is mainly found along river banks. Riparian systems are especially prone to invasion as their dynamic physical nature provides suitable conditions for introduced species due to periodic nutrient enrichment, open available space, and availability of light and moisture for the successful germination of seedlings (Hupp and Osterkamp, 1996). Colonisation and subsequent spread of *I. glandulifera* in river catchments is driven by occasional dispersal events mediated by human activity (Walker *et al.*, 2009). Along the same river system, genetic diversity in the downstream populations higher compared to upstream populations (Love *et al.*, 2013). Genetic analysis of *I. glandulifera* populations in Lithuania showed significant genetic differentiation between populations (Zybartaite *et al.*, 2011).

Pahl *et al*. (2013) find no evidence of local adaptation in *I. glandulifera* and suggest that the species is coping with heterogeneous environments with higher phenotypic plasticity of traits. Skálová *et al*. (2012, 2013) find that invasive *Impatiens* species show higher plasticity of traits than a native congener, whereas Skálová *et al*. (2011) studying germination, seedling emergence and seedling frost resistance in native and invasive *Impatiens* species, find indications of local adaptation in invasive *I. parviflora* and *I. glandulifera*. Kollmann & Bañuelos (2004) studied patterns of morphological and phenological trait variation on populations sampled along a latitudinal gradient in a common garden. They find latitudinal clines in morphological and phenological traits and suggest that the observed clines are an indication of adaptive responses to the length of growing season.

When co-occurring, the native species shows decreased performance in comparison with the invasive species and the native species will be out-competed by the invading congener (Skálová *et al.*, 2013, Čuda *et al.*, 2014). Godefroid & Koedam (2010) and Vervoort *et al.* (2011)) studied comparative ecology and coexistence of *I. noli-tangere* and *I. parviflora* in Belgium and find that *I. parviflora* prefers soils with low nitrogen and that there is some overlap in habitat between these two species. They find no indication of a negative effect of *I. parviflora* on the cover of *I. noli-tangere*.

Study area and populations

In July 2011, we collected samples from six populations of *I. glandulifera* in its native habitat, Kashmir, India. In July–August 2011, we sampled 4–6 populations of each of the three *Impatiens* species from an approximately 1600 km long latitudinal gradient from northern France (49°34'N) in the south to Trondheim, Norway (63°40'N) in the north (Figure 5). We did not find suitable populations of *I. parviflora* in northern France and the species does not occur in Trondheim (http://artskart.artsdatabanken.no/FaneKart.aspx). Furthermore, we could not sample *I. noli-tangere* in Stockholm, Sweden because most populations were disturbed by wild animals. In each region, we sampled the populations within an area of *ca.* 30 km × 30 km. The populations within each region were separated by a minimum of 500 m. Within each population, we selected a 25 m × 25 m quadrat for sampling. We measured nitrogen content in the soil and average temperature for six weeks during the growing season. We also noted habitat type: riverbank, lakeshore, forest edge, forest interior, roadside, garden etc.

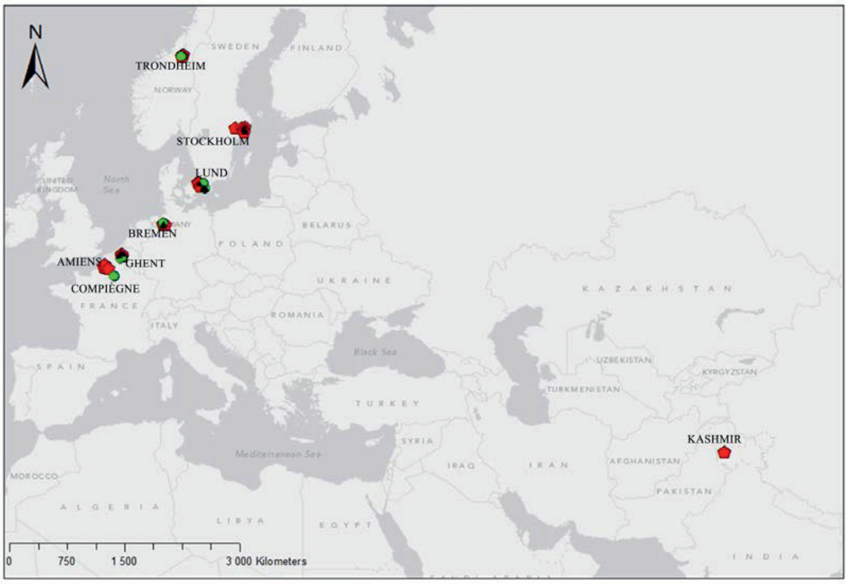

Figure 5: Regions where populations were sampled (Red – *Impatiens glandulifera,* Green – *I. noli-tangere*, Black – *I. parviflora*).

Specific methods

Genetic diversity

For studying genetic diversity between native and invasive populations of *I. glandulifera,* we chose ten populations from the invaded range along a 1600 km latitudinal gradient in western Europe and three populations from the native range in Kashmir, India. We collected leaf material from 30 individuals in each population. Because of fungal infection, we could only use 20 individuals for one population from Kashmir giving a total of 380 individuals analysed. We extracted total DNA and calculated genetic diversity (h) between individuals from different populations. We used the software BOTTLENECK v 1.2.02 (Cornuet and Luikart, 1996) to detect recent population bottlenecks among the studied populations, the software STRUCTURE v 2.2 (Pritchard *et al.*, 2000, Falush *et al.*, 2003) to examine geographic clustering of the genetic diversity and DISTRUCT v 1.1 (Rosenberg, 2004) for graphical presentation of the results.

Greenhouse experiments

We ran two experiments in the greenhouse on *I. glandulifera*; (a) to study whether the plants are pre-adapted to attain their observed size and reproduction strategy and plasticity within the invaded range (Paper **II**), and (b) to study rapid local adaptation (Paper **III**). After selecting populations (see below for details), 30 seeds from each mother plant were stratified at 4°C. After germination, seedlings were planted in the greenhouse of Department of Biology, NTNU. I briefly describe the experiment set up for each of the two greenhouse studies.

For the first study (Paper **II**), we chose two populations from Trondheim (invasive range) and from Kashmir, India (native range). These populations were selected on the basis of varying soil nitrogen and more-or-less similar habitat type in the field. We randomly selected 20 individuals per population. Three seedlings from each of the 20 individuals were subjected to one of three environments (high nutrient, medium nutrient, and low nutrient). This resulted in a total of 240 individuals (2 ranges × 2 populations × 20 mother plants × 3 treatments). Plants were grown at 18°C during the day and 8°C during night with a L:D cycle of 12:12h. We performed cross-pollination between individuals from the same populations and measured morphological and phenological traits.

For the second study (Paper **III**), we chose one population from each of six regions from the invasive range of *I. glandulifera*. These populations were chosen on the basis of plant height which showed average plant height closest to the grand mean of all 36 populations. This resulted in a total of 180 individuals (6 regions × 30 individuals). Individuals from each population were randomly placed on eight trays in two rooms. Plants were grown at 18°C during the day and 8°C during night with a L:D cycle of 12:12h. Plants were fertilised once a week for 20 minutes and for the rest of the time, the trays were filled with about 5 cm standing water. We grew the plants for two generations.

Trait measurements in the wild and in the greenhouse

In the greenhouse, at least 10 flowers of each individual were cross-pollinated with pollen from randomly selected individuals from the same population. At the end of the growing season, we measured plant height (excluding inflorescences) (Cornelissen *et al.*, 2003), counted total number of flowers, collected all matured capsules and harvested the above-ground parts. The harvested above-ground parts were oven dried at 60°C for 72 hours and weighed to calculate above-ground biomass. Table 1 lists the morphological and phenological traits we measured in the wild populations and in the greenhouse.

Table 1: Lists of traits measured in the wild and in the greenhouse

Species	Traits	Wild	Greenhouse
I. noli-tangere & I. parviflora	Plant height	√	
	Leaf area	√	
	Seed mass	√	
	Seeds per capsule	√	
I. glandulifera	Plant height	√	√
	Seed mass	√	√
	Seeds per capsule	√	√
	Above-ground biomass	√	√
	Number of nodes		√
	Days to first flower		√
	Flowers produced		√
	Reproductive output		√

MAIN RESULTS AND DISCUSSION

Strong loss in genetic diversity of *Impatiens glandulifera* despite multiple introductions (Paper I)

In paper **I** we studied genetic diversity in the native and invasive populations of *I. glandulifera*. We find a strong loss in average genetic diversity both at the within-population (Europe: 0.210; Kashmir: 0.629) (t-test $p < 0.001$) and at the between-population level (Europe: 0.351; Kashmir: 0.779) (Wilcoxon rank sum test $p < 0.001$) in the invasive populations compared to the native populations. Among European populations, we observed two clear clusters, one containing the southern European populations (south of Lund to France) and the other cluster containing the northern European populations (Stockholm and Trondheim) suggesting different introductions of the north and south European populations.

These results indicate that even after multiple introductions, the genetic diversity is lower in the invasive populations than in the native populations. This can partly be explained by high interannual variation in population size in *I. glandulifera* (Walker *et al.*, 2009, Gederaas *et al.*, 2012), leading to high genetic drift. Analysis of molecular variance (AMOVA) and the fixation index (F_{ST}), a measure of population differentiation due to genetic structure, show that most of the genetic diversity is found within populations compared to between populations. This indicates high levels of gene flow, in particular between the Kashmir populations. Evidence of gene flow is low in its invaded environment. This is further supported by adaptive genetic differentiation observed for plant height and time to first flower (Paper III). A study by Zybartaite *et al.* (2011) also found significant genetic differentiation of *I. glandulifera* populations in Lithuania.

Genetic shift after introduction vs pre-adaptation in *Impatiens glandulifera* (Paper II)

In paper **II** we studied whether high competitiveness, abundant reproduction and high plasticity of traits in invasive *I. glandulifera* have evolved after their introduction into new environments, such that they differ ecologically from conspecifics growing in the species' native range (genetic shift) or whether they were already present in the native range (pre-adaptation) by comparing populations from native and invasive ranges grown under three different nutrient treatments. We find no significant difference in vegetative growth and reproductive output between the invasive and the native populations of *I. glandulifera* suggesting that these traits would not form the basis of any competitive advantage conferring invasiveness. Furthermore, we find no significant difference in plasticity of plant height, above-ground biomass, seed mass and flowers produced. In these traits neither the slope nor the curvature of the reaction norm differs between populations. For the number of nodes, the curvature of the reaction norm is more pronounced in the invasive populations, which indicates evolution of high plasticity of this trait after introduction.

Larger size and higher biomass are likely to promote the competitive ability of plants, and therefore likely to promote invasiveness (Baker, 1974, van Kleunen *et al.*, 2007, Van Kleunen *et al.*, 2010). The lack of a significant difference in plant height and above-ground biomass between our native and invasive populations could be because the invasive populations were from the northern end of the invasive distribution (Trondheim, Norway) (Beerling and Perrins, 1993) and the short length of the growing season could explain the lower plant height and above-ground biomass in the invasive range (Paper **III**). Fewer numbers of seeds per capsule in the invasive range than in the native range both in the wild and in the greenhouse implies that this trait is genetically determined with little genetic variation rather than environmental effect (cf. Kollmann *et al.*, 2007), which is further supported by the lack of treatment effect for this trait in the greenhouse. Interestingly, the observed difference in seed mass between native and invasive ranges disappeared in the greenhouse, which indicates that this trait is more affected by the environment than by genetics.

Except for number of nodes, we find no significant difference in plasticity of traits. For the traits that we measured, it clearly shows that these traits are pre-adaptive for the species to become invasive elsewhere (e.g. Schlaepfer *et al.*, 2010, van Kleunen *et al.*, 2011). Furthermore, during filtering out after introduction, pre-adapted genotypes might have become successful invaders in Europe (e.g. Bossdorf *et al.*, 2008).

The invasive populations have lower reproductive output which might lower fitness. However, the species is widely distributed across Europe. Wider distribution of this species might be linked to the higher seed mass observed in the wild. Since invasive species often occupy nutrient-rich soils, seed mass might have played a role in the success of this species.

Local adaptation in the invasive *Impatiens glandulifera* (Paper III)

Impatiens glandulifera was introduced about 160 years ago in Europe and is now widely distributed in many countries. Therefore, this species is a suitable study system to investigate the evolution of local adaptation (cf. Sax *et al.*, 2007). In paper **III** we studied whether the wider distribution of this species along a latitudinal gradient is due to local adaptation or phenotypic plasticity. We answered this by growing *I. glandulifera* collected from different regions along a latitudinal gradient in western Europe in a greenhouse in Trondheim, Norway for two generations. We observed adaptive genetic differentiation of plant height, number of days to first flower, and partly, number of nodes and total number of flowers produced with latitude. Although we cannot rule out local adaption on seed mass, it appears that environmental variation possibly results in systematic differences between populations in this trait.

The latitudinal clines observed for plant height and numbers of days to first flower were conserved in both the generations. This indicates an adaptive response to the shorter length of the growing season with increasing latitude. The length of the growing season decreases with increasing latitude which constrains the period available for growth, flowering and maturation of seeds. Earlier flowering at shorter height can also be an adaptive trade-off between allocation to reproduction and vegetative growth (Reznick *et al.*, 2000). Earlier flowering in the northern populations may reduce the resources available for vegetative growth and allocate it to reproductive output.

For the number of nodes and the total number of flowers produced, a significant latitude × generation interaction suggests that part of the variation is also due to phenotypic plasticity. Furthermore, no significant correlation between generations in the population mean residuals of the linear models indicates that the patterns of variation are not genetically determined. Interestingly, the relationship between plant height and above-ground biomass in this species is not correlated. Plant height and above-ground biomass are often correlated in annual species (e.g. Gross and Soule, 1981, Samson and Werk, 1986). Lack of correlation between these two traits might be because the northern individuals were more branched than populations from southern latitudes. This is reflected by the total number of flowers produced which increased with increasing latitude.

Seed mass is one of the most important traits for seedling and overall plant performance (Baskin and Baskin, 1973). Although growth and phenological traits show latitudinal clines, seed mass did not show a significant latitudinal cline. As suggested by Wulff (1986), the absence of a latitudinal cline for seed mass might reflect that this trait is more dependent on environmental conditions (e.g. nutrient, water supply) than genetics.

These findings suggest that the recent colonisation of this species in northern Europe is associated with the evolution of several life-history traits and shows a strong capacity for this species to adapt to new conditions not encountered in its native environment.

Is invasive *Impatiens parviflora* more responsive to nitrogen and/or temperature than the native *I. noli-tangere*? (Paper IV).

Shifts in magnitude and variability of global change drivers such as nitrogen deposition or climate warming may provide colonisation opportunities and promote the spread of invasive species (Davis *et al.*, 2000, Dukes *et al.*, 2011). This is because invasive species are thought to be better at acquiring resources than native species (Vitousek, 1986, Lowe *et al.*, 2003). We compared trait variation in native and invasive species along a latitudinal gradient. Such comparisons provide an opportunity to elucidate variation in plant traits and unravel the relative importance of environmental factors (soil nutrients, temperature, etc.) (De Frenne *et al.*, 2013). We found that both the native and invasive species are taller towards higher latitudes with stronger responses in the invasive species, whereas seed mass and seeds per capsule responded in opposite directions; both traits increase in the native species and decrease in the invasive species with increasing latitude.

Soil nitrogen is negatively correlated with latitude for the growing sites of both species. Performance of the invasive species in terms of plant height decreases with increasing nitrogen. This is in contrast to the general trend reported in the literature between plant height and soil nitrogen. This converse trend might be because other factors interacting with soil nitrogen affect plant height rather than simply soil nitrogen in the strict sense (Peace and Grubb, 1982). Furthermore, our results indicate that the invasive species is better at allocating available resources to plant size which may provide a competitive advantage for light over co-occurring species (Graebner *et al.*, 2012).

Production of heavier seeds by taller plants with increasing latitude may be an adaptive response to establishment in the relatively harsher climatic conditions towards the north (Moles and Westoby, 2003). In the invasive species, taller plants produced seeds with lower seed mass. As both species have explosive seed dispersal mechanism (ballochory), taller invasive species with lighter seeds can be dispersed over greater distances. This might increase the further spread of the invasive species.

We found no relationship between plant traits and microclimate during the growing season. This could be because we measured temperature only during six weeks of the growing season and temperatures outside the measured period most likely also affect plant growth.

CONCLUSIONS AND FUTURE PERSPECTIVES

This thesis demonstrates several important aspects of invasion ecology. The study on genetic diversity between native and invasive populations shows evidence of multiple introductions of the invasive *I. glandulifera* in Europe. Despite multiple introductions, there is a strong loss of genetic diversity in the invasive populations compared to the native populations. However, the loss of genetic diversity in the invasive populations does not constrain evolution of adaptive genetic differentiation. The greenhouse study on trait variation of this species shows adaptive evolution (genetic differentiation) along the latitudinal gradient. Furthermore, the study on genetic shifts after introduction or pre-adaptation shows that most of the traits are pre-adapted which favour this species becoming invasive elsewhere. Although pre-adapted, the invasive populations seem to have poorer seed-set in the invasive range which indicates that they lose some power after introduction. Our results also show that the invasive species has a strong capacity to adapt to new conditions. If care is not taken, high probability of additional introductions into areas which have higher levels of commercial trade and transport, increases the chances of further spread. The comparative study between a native and an invasive species shows that the performance of the invasive species in terms of plant height is better under low nitrogen conditions along a latitudinal gradient indicating that the invasive species is not constrained by low nitrogen conditions.

A major challenge in managing and controlling invasive species lies ahead in virtually every ecosystem through-out the world. It is clearly desirable to eliminate invasive species as soon as possible after the invasion, before they adapt to the introduced environment and before additional invasions occur. Unfortunately this is rarely achieved. Understanding genetics and evolution of (potential) introduced species may help to single out invasive species and allow for restrictions on transport or for proper management strategies to be implemented, including prevention of introductions and control of established populations.

The thesis shows ecoevolutionary phenomena of invasive species. Future research would be to study colonisation capacity and impact of the invasive species in different habitats. As invasive species cannot be planted in a natural environment because of ethical and legal reasons, this could be done in a controlled environment by sowing seeds of the invasive species into transplanted vegetation patches simulating different natural plant communities. In paper I, we attempted to make inferences about invasion pathways and colonisation processes, such as the amount of loss of genetic diversity during colonization. However, including fewer sampling populations from its native range limited our ability to make those inferences. A wider sampling from its native range and invasive range would help to identify possible invasion pathways and colonisation processes. In paper IV, we attempted to find which factor/s are important for traits of both the native and invasive species. We found that these patterns are not straightforward. Future studies are needed to unravel these mechanisms and to predict whether invasiveness will be favoured by warming. This can be studied by measuring temperatures at the population sites for a longer period preferable all year around and for several years. Identifying source, invasion pathways, colonisation processes and/or vegetation interaction can help to design effective control programs (Rollins *et al.*, 2009) and prevent or limit introduction via potential routes of introduction.

REFERENCES

Allendorf, F. W. & Lundquist, L. L. (2003) Introduction: population biology, evolution, and control of invasive species. *Conservation Biology,* **17,** 24-30.

Amsellem, L., Noyer, J. L., Le Bourgeois, T. & Hossaert-McKey, M. (2000) Comparison of genetic diversity of the invasive weed *Rubus alceifolius* Poir. (Rosaceae) in its native range and in areas of introduction, using amplified fragment length polymorphism (AFLP) markers. *Molecular Ecology,* **9,** 443-455.

Andrews, M., Maule, H. G., Raven, J. A. & Mistry, A. (2005) Extension growth of *Impatiens glandulifera* at low irradiance: Importance of nitrate and potassium accumulation. *Annals of Botany,* **95,** 641-648.

Baker, H. G. (1965) Characteristics and modes of origin of weeds. *The genetics of colonizing species.* (eds H. G. Baker & G. L. Stebbins), pp. 147-169. Academic Press, New York.

Baker, H. G. (1974) The evolution of weeds. *Annual Review of Ecology and Systematics***,** 1-24.

Barrett, S. C. & Kohn, J. R. (1991) Genetic and evolutionary consequences of small population size in plants. *Genetics and Conservation of Rare Plants* (eds D. A. Falk & K. E. Holsinger), pp. 3-30. New York: Oxford University Press.

Baskin, J. M. & Baskin, C. C. (1973) Plant population differences in dormancy and germination characteristics of seeds: heredity or environment? *American midland naturalist***,** 493-498.

Beerling, D. J. & Perrins, J. M. (1993) *Impatiens glandulifera* Royle (Impatiens-Roylei Walp). *Journal of Ecology,* **81,** 367-382.

Blanquart, F., Kaltz, O., Nuismer, S. L. & Gandon, S. (2013) A practical guide to measuring local adaptation. *Ecology Letters,* **16,** 1195-1205.

Bossdorf, O., Lipowsky, A. & Prati, D. (2008) Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. *Diversity and Distributions,* **14,** 676-685.

Bradshaw, A. D. (1965) Evolutionary significance of phenotypic plasticity. *Advances in Genetics,* **13,** 115-155.

Bradshaw, W. & Holzapfel, C. (2008) Genetic response to rapid climate change: it's seasonal timing that matters. *Molecular Ecology,* **17,** 157-166.

Caño, L., Escarre, J., Fleck, I., Blanco-Moreno, J. M. & Sans, F. X. (2008) Increased fitness and plasticity of an invasive species in its introduced range: a study using *Senecio pterophorus*. *Journal of Ecology,* **96,** 468-476.

Clegg, S. M., Degnan, S. M., Kikkawa, J., Moritz, C., Estoup, A. & Owens, I. P. (2002) Genetic consequences of sequential founder events by an island-colonizing bird. *Proceedings of the National Academy of Sciences of the United States of America,* **99,** 8127-8132.

Clifton, R. (2000) Geraniales Species Check List Series: vol. 6. Geraniaceae Bentham and Hooker, tribe VII Balsamineae. Dover: Geraniaceae Group 90p.

Colautti, R. I. & Barrett, S. C. H. (2013) Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science,* **342,** 364-366.

Colautti, R. I. & MacIsaac, H. J. (2004) A neutral terminology to define 'invasive' species. *Diversity and Distributions,* **10,** 135-141.

Coombe, D. E. (1956) *Impatiens Parviflor*a DC. *Journal of Ecology,* **44,** 701-713.

Cornelissen, J., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D., Reich, P., ter Steege, H., Morgan, H. & Van Der Heijden, M. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany,* **51,** 335-380.

Cornuet, J. M. & Luikart, G. (1996) Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics,* **144,** 2001-2014.

Čuda, J., Skálová, H., Janovský, Z. & Pyšek, P. (2014) Habitat requirements, short-term population dynamics and coexistence of native and invasive Impatiens species: a field study. *Biological Invasions,* **16,** 177-190.

Daehler, C. C. (2003) Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology Evolution and Systematics,* **34,** 183-211.

Daneshgar, P. & Jose, S. (2009) Mechanisms of plant invasion: A Review. *Invasive Plants and Forest Ecosystems* (eds R. K. Kohli, S. Jose, H. P. Singh & D. R. Batish), pp. 11-27. CRC Press, Taylor & Francis Group, NW.

Davidson, A. M., Jennions, M. & Nicotra, A. B. (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters,* **14,** 419-431.

Davis, M. A., Grime, J. P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology,* **88,** 528-534.

De Frenne, P., Graae, B. J., Rodríguez-Sánchez, F., Kolb, A., Chabrerie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., Eriksson, O., Gruwez, R., Hermy, M., Lenoir, J., Plue, J., Coomes, D. A. & Verheyen, K. (2013) Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology,* **101,** 784-795.

DeWalt, S. J., Denslow, J. S. & Ickes, K. (2004) Natural-enemy release facilitates habitat expansion of the invasive tropical shrub Clidemia hirta. *Ecology,* **85,** 471-483.

DeWitt, T. J. & Scheiner, S. M. (2004) *Phenotypic Plasticity: Functional and Conceptual Approaches.* Oxford University Press Oxford.

Dlugosch, K. M. & Parker, I. M. (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology,* **17,** 431-449.

Dukes, J. S., Chiariello, N. R., Loarie, S. R. & Field, C. B. (2011) Strong response of an invasive plant species (*Centaurea solstitialis* L.) to global environmental changes. *Ecological Applications,* **21,** 1887-1894.

Elemans, M. (2004) Light, nutrients and the growth of herbaceous forest species. *Acta Oecologica,* **26,** 197-202.

Ellstrand, N. C. & Schierenbeck, K. A. (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences,* **97,** 7043-7050.

Elton, C. S. (1958) *The Ecology of Invasions by Animals and Plants.* Methuen, London.

Endler, J. A. (1977) *Geographic variation, speciation, and clines.* Princeton University Press, Princeton, N.J.

Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Hülber, K., Jarošík, V., Kleinbauer, I., Krausmann, F., Kühn, I., Nentwig, W., Vilà, M., Genovesi, P., Gherardi, F., Desprez-Loustau, M.-L., Roques, A. & Pyšek, P. (2011) Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences of the United States of America,* **108,** 203-207.

Estoup, A., Beaumont, M., Sennedot, F., Moritz, C. & Cornuet, J. M. (2004) Genetic analysis of complex demographic scenarios: Spatially expanding populations of the cane toad, *Bufo marinus*. *Evolution,* **58,** 2021-2036.

Falk-Petersen, J., Bøhn, T. & Sandlund, O. (2006) On the Numerous Concepts in Invasion Biology. *Biological Invasions,* **8,** 1409-1424.

Falush, D., Stephens, M. & Pritchard, J. K. (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics,* **164,** 1567-1587.

Frankham, R. (2005) Invasion biology - Resolving the genetic paradox in invasive species. *Heredity,* **94,** 385-385.

Funk, J. L. (2008) Differences in plasticity between invasive and native plants from a low resource environment. *Journal of Ecology,* **96,** 1162-1173.

Gederaas, L., Moen, T., Skjelseth, S. & Larsen, L. (2012) Fremmede arter i Norge–med norsk svarteliste 2012. *Artsdatabanken, Trondheim,* **20,** 2012.

Genton, B. J., Shykoff, J. A. & Giraud, T. (2005) High genetic diversity in French invasive populations of common ragweed, *Ambrosia artemisiifolia*, as a result of multiple sources of introduction. *Molecular Ecology,* **14,** 4275-4285.

Ghalambor, C. K., McKay, J. K., Carroll, S. P. & Reznick, D. N. (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology,* **21,** 394-407.

Glowka, L., Burhenne-Guilmin, F. & Synge, H. (1994) A Guide to the convention on biological diversity. IUCN Gland and Cambridge. xii + 161pp.

Godefroid, S. & Koedam, N. (2010) Comparative ecology and coexistence of introduced and native congeneric forest herbs: *Impatiens parviflora* and *I. noli-tangere*. *Plant Ecology and Evolution,* **143,** 119-127.

Graae, B. J., De Frenne, P., Kolb, A., Brunet, J., Chabrerie, O., Verheyen, K., Pepin, N., Heinken, T., Zobel, M., Shevtsova, A., Nijs, I. & Milbau, A. (2012) On the use of weather data in ecological studies along altitudinal and latitudinal gradients. *Oikos,* **121,** 3-19.

Graebner, R. C., Callaway, R. M. & Montesinos, D. (2012) Invasive species grows faster, competes better, and shows greater evolution toward increased seed size and growth than exotic non-invasive congeners. *Plant Ecology,* **213,** 545-553.

Gross, K. L. & Soule, J. D. (1981) Differences in biomass allocation to reproductive and vegetative structures of male and female plants of a dioecious, perennial herb, *Silene alba* (Miller) Krause. *American Journal of Botany,* **68,** 801-807.

Hatcher, P. E. (2003) *Impatiens noli-tangere* L. *Journal of Ecology,* **91,** 147-167.

Hejda, M., Pysek, P., Pergl, J., Sadlo, J., Chytry, M. & Jarosik, V. (2009) Invasion success of alien plants: do habitat affinities in the native distribution range matter? *Global Ecology and Biogeography,* **18,** 372-382.

Hierro, J. L., Maron, J. L. & Callaway, R. M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology,* **93,** 5-15.

Hulme, P. E. (2008) Phenotypic plasticity and plant invasions: is it all Jack? *Functional Ecology,* **22,** 3-7.

Hupp, C. R. & Osterkamp, W. (1996) Riparian vegetation and fluvial geomorphic processes. *Geomorphology,* **14,** 277-295.

Janssens, S., Geuten, K., Yuan, Y.-M., Song, Y., Küpfer, P. & Smets, E. (2006) Phylogenetics of *Impatiens* and *Hydrocera* (Balsaminaceae) using chloroplast atpB-rbcL spacer sequences. *Systematic Botany,* **31,** 171-180.

Jørgensen, C. A. (1926) *Impatiens parviflora* DC i Denmark. *Botanisk Tidsskrifter,* **39,** 385-389.

Kattge, J., DÍAz, S., Lavorel, S., Prentice, I. C., Leadley, P., BÖNisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Van Bodegom, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., Atkin, O., Bahn, M., Baker, T. R., Baldocchi, D., Bekker, R., Blanco, C. C., Blonder, B., Bond, W. J., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender-Bares, J., Chambers, J. Q., Chapin Iii, F. S., Chave, J., Coomes, D., Cornwell, W. K., Craine, J. M., Dobrin, B. H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W. F., Fang, J., FernÁNdez-MÉNdez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G. T., Fyllas, N. M., Gallagher, R. V., Green, W. A., Gutierrez, A. G., Hickler, T., Higgins, S. I., Hodgson, J. G., Jalili, A., Jansen, S., Joly, C. A., Kerkhoff, A. J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J. M. H., Kramer, K., KÜHn, I., Kurokawa, H., Laughlin, D., Lee, T. D., Leishman, M., Lens, F., Lenz, T., Lewis, S. L., Lloyd, J., LlusiÀ, J., Louault, F., Ma, S., Mahecha, M. D., Manning, P., Massad, T., Medlyn, B. E., Messier, J., Moles, A. T., MÜLler, S. C., Nadrowski, K., Naeem, S., Niinemets, Ü., NÖLlert, S., NÜSke, A., Ogaya, R., Oleksyn, J., Onipchenko, V. G., Onoda, Y., OrdoÑEz, J., Overbeck, G., Ozinga, W. A., et al. (2011) TRY – a global database of plant traits. *Global Change Biology,* **17,** 2905-2935.

Kawecki, T. J. & Ebert, D. (2004) Conceptual issues in local adaptation. *Ecology Letters,* **7,** 1225-1241.

Keane, R. M. & Crawley, M. J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution,* **17,** 164-170.

Kinziger, A. P., Nakamoto, R. J., Anderson, E. C. & Harvey, B. C. (2011) Small founding number and low genetic diversity in an introduced species exhibiting limited invasion success (speckled dace, *Rhinichthys osculus*). *Ecology and Evolution,* **1,** 73-84.

Kolar, C. S. & Lodge, D. M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution,* **16,** 199-204.

Kolbe, J. J., Glor, R. E., Schettino, L. R., Lara, A. C., Larson, A. & Losos, J. B. (2004) Genetic variation increases during biological invasion by a Cuban lizard. *Nature,* **431,** 177-181.

Kollmann, J. & Banuelos, M. J. (2004) Latitudinal trends in growth and phenology of the invasive alien plant *Impatiens glandulifera* (Balsaminaceae). *Diversity and Distributions,* **10,** 377-385.

Kollmann, J., Bañuelos, M. J. & Nielsen, S. L. (2007) Effects of virus infection on growth of the invasive alien *Impatiens glandulifera*. *Preslia,* **79,** 33-44.

Körner, C. (2007) The use of ‘altitude’in ecological research. *Trends in Ecology & Evolution,* **22,** 569-574.

Lamarck, J. (1809) *Philosophical Zoology: An Exposition with Regard to the Natural History of Animals.* University of Chicago Press, Chicago, USA.

Lambdon, P. W., Pysek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F., Jarosik, V., Pergl, J., Winter, M., Anastasiu, P., Andriopoulos, P., Bazos, I., Brundu, G., Celesti-Grapow, L., Chassot, P., Delipetrou, P., Josefsson, M., Kark, S., Klotz, S., Kokkoris, Y., Kuehn, I., Marchante, H., Perglova, I., Pino, J., Vila, M., Zikos, A., Roy, D. & Hulme, P. E. (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia,* **80,** 101-149.

Lambrinos, J. G. (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology,* **85,** 2061-2070.

Lavergne, S. & Molofsky, J. (2007) Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proceedings of the National Academy of Sciences of the United States of America,* **104,** 3883-3888.

Lee, C. E. (2002) Evolutionary genetics of invasive species. *Trends in Ecology & Evolution,* **17,** 386-391.

Lee, C. E. & Gelembiuk, G. W. (2008) Evolutionary origins of invasive populations. *Evolutionary Applications,* **1,** 427-448.

Leimu, R. & Fischer, M. (2008) A meta-analysis of local adaptation in plants. *PLoS One,* **3,** e4010.

Leishman, M. R., Wright, I. J., Moles, A. T. & Westoby, M. (2000) The evolutionary ecology of seed size. *Seeds: The Ecology of Regeneration in Plant Communities* (ed M. Fenner), pp. 31-57. CAB International, Wallingford, UK.

Li, B., Suzuki, J.-I. & Hara, T. (1998) Latitudinal variation in plant size and relative growth rate in *Arabidopsis thaliana*. *Oecologia,* **115,** 293-301.

Love, H. M., Maggs, C. A., Murray, T. E. & Provan, J. (2013) Genetic evidence for predominantly hydrochoric gene flow in the invasive riparian plant *Impatiens glandulifera* (Himalayan balsam). *Annals of Botany,* **112,** 1743-1750.

Lowe, P., Lauenroth, W. & Burke, I. (2003) Effects of nitrogen availability on competition between *Bromus tectorum* and *Bouteloua gracilis*. *Plant Ecology,* **167,** 247-254.

Macel, M., Lawson, C. S., Mortimer, S. R., Smilauerova, M., Bischoff, A., Crémieux, L., Doležal, J. í., Edwards, A. R., Lanta, V. & Bezemer, T. M. (2007) Climate vs. soil factors in local adaptation of two common plant species. *Ecology,* **88,** 424-433.

Mack, R. N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M. & Bazzaz, F. A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological applications,* **10,** 689-710.

Markov, M. (1991) Population biology of touch-me-not balsam *Impatiens noli-tangere* L. *Soviet Journal of Ecology,* **22,** 12-20.

Maron, J. L., Vila, M., Bommarco, R., Elmendorf, S. & Beardsley, P. (2004) Rapid evolution of an invasive plant. *Ecological Monographs,* **74,** 261-280.

Mason, R. A. B., Cooke, J., Moles, A. T. & Leishman, M. R. (2008) Reproductive output of invasive versus native plants. *Global Ecology and Biogeography,* **17,** 633-640.

Masuda, M. & Yahara, T. (1994) Reproductive ecology of a cleistogamous annual, *Impatiens noli-tangere* L., occuring under different environmental conditions. *Ecological Research,* **9,** 67-75.

Mazza, G., Tricarico, E., Genovesi, P. & Gherardi, F. (2014) Biological invaders are threats to human health: an overview. *Ethology Ecology & Evolution,* **26,** 112-129.

McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution,* **21,** 178-185.

Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., Pitman, A., Hemmings, F. A. & Leishman, M. R. (2009) Global patterns in plant height. *Journal of Ecology,* **97,** 923-932.

Moles, A. T. & Westoby, M. (2003) Latitude, seed predation and seed mass. *Journal of Biogeography,* **30,** 105-128.

Montague, J. L., Barrett, S. C. H. & Eckert, C. G. (2008) Re-establishment of clinal variation in flowering time among introduced populations of purple loosestrife (*Lythrum salicaria*, Lythraceae). *Journal of Evolutionary Biology,* **21,** 234-245.

Monty, A., Bizoux, J. P., Escarre, J. & Mahy, G. (2013) Rapid plant invasion in distinct climates involves different sources of phenotypic variation. *PLoS One,* **8,** e55627.

Nagy, A.-M. & Korpelainen, H. (2014) Population genetics of Himalayan balsam (*Impatiens glandulifera*): comparison of native and introduced populations. *Plant Ecology and Diversity***,** 1-5.

Nei, M., Maruyama, T. & Chakraborty, R. (1975) The bottleneck effect and genetic variability in populations. *Evolution,* **29,** 1-10.

Novak, S. J. & Mack, R. N. (1993) Genetic variation in *Bromus tectorum* (Poaceae): comparison between native and introduced populations. *Heredity,* **71,** 167-176.

Öckinger, E., Schweiger, O., Crist, T. O., Debinski, D. M., Krauss, J., Kuussaari, M., Petersen, J. D., Pöyry, J., Settele, J., Summerville, K. S. & Bommarco, R. (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology Letters,* **13,** 969-979.

Pahl, A. T., Kollmann, J., Mayer, A. & Haider, S. (2013) No evidence for local adaptation in an invasive alien plant: field and greenhouse experiments tracing a colonization sequence. *Annals of Botany,* **112,** 1921-1930.

Peace, W. J. H. & Grubb, P. J. (1982) Interaction of light and mineral nutrient supply in the growth of *Impatiens parviflora*. *New Phytologist,* **90,** 127-150.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J. G., Thompson, K., Morgan, H. D., ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A. C., Aquino, S. & Cornelissen, J. H. C. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany,* **61,** 167.

Perrins, J., Fitter, A. & Williamson, M. (1993) Population biology and rates of invasion of 3 introduced *Impatiens* species in the British Isles. *Journal of Biogeography,* **20,** 33-44.

Pigliucci, M. (2001) *Phenotypic Plasticity: Beyond Nature and Nurture.* JHU Press.

Polunin, O. & Stainton, A. (1984) *Flowers of the Himalaya.* Oxford University Press, Dehli.

Pritchard, J. K., Stephens, M. & Donnelly, P. (2000) Inference of population structure using multilocus genotype data. *Genetics,* **155,** 945-959.

Pyšek, P. & Prach, K. (1995) Invasion dynamics of *Impatiens glandulifera* - a century of spreading reconstructed. *Biological Conservation,* **74,** 41-48.

Pyšek, P. & Richardson, D. (2007) Traits associated with invasiveness in alien plants: Where do we stand? *Biological Invasions* (ed N. W.), pp. 97-125. Springer-Verlag,, Berlin & Heidelberg.

Qing, H., Yao, Y., Xiao, Y., Hu, F., Sun, Y., Zhou, C. & An, S. (2011) Invasive and native tall forms of Spartina alterniflora respond differently to nitrogen availability. *Acta Oecologica,* **37,** 23-30.

Reich, P. B. & Oleksyn, J. (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America,* **101,** 11001-11006.

Rejmánek, M. & Richardson, D. M. (1996) What attributes make some plant species more invasive? *Ecology,* **77,** 1655-1661.

Reznick, D., Nunney, L. & Tessier, A. (2000) Big houses, big cars, superfleas and the costs of reproduction. *Trends in Ecology & Evolution,* **15,** 421-425.

Richards, C. L., Bossdorf, O., Muth, N. Z., Gurevitch, J. & Pigliucci, M. (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters,* **9,** 981-993.

Richardson, D. M., Pysek, P., Rejmanek, M., Barbour, M. G., Panetta, F. D. & West, C. J. (2000) Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions,* **6,** 93-107.

Rollins, L. A., Woolnough, A. P., Wilton, A. N., Sinclair, R. O. N. & Sherwin, W. B. (2009) Invasive species can't cover their tracks: using microsatellites to assist management of starling (*Sturnus vulgaris*) populations in Western Australia. *Molecular Ecology,* **18,** 1560-1573.

Rosenberg, N. A. (2004) DISTRUCT: a program for the graphical display of population structure. *Molecular Ecology Notes,* **4,** 137-138.

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N. & Weller, S. G. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics,* **32,** 305-332.

Samson, D. A. & Werk, K. S. (1986) Size-Dependent Effects in the Analysis of Reproductive Effort in Plants. *The American Naturalist,* **127,** 667-680.

Sax, D. F., Stachowicz, J. J., Brown, J. H., Bruno, J. F., Dawson, M. N., Gaines, S. D., Grosberg, R. K., Hastings, A., Holt, R. D. & Mayfield, M. M. (2007) Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution,* **22,** 465-471.

Schlaepfer, D. R., Glättli, M., Fischer, M. & van Kleunen, M. (2010) A multi-species experiment in their native range indicates pre-adaptation of invasive alien plant species. *New Phytologist,* **185,** 1087-1099.

Schlichting, C. D. & Levin, D. A. (1986) Phenotypic plasticity: an evolving plant character. *Biological Journal of the Linnean Society,* **29,** 37-47.

Shipley, B. & Dion, J. (1992) The allometry of seed production in herbaceous angiosperms. *American Naturalist***,** 467-483.

Shirk, R., Hamrick, J., Zhang, C. & Qiang, S. (2014) Patterns of genetic diversity reveal multiple introductions and recurrent founder effects during range expansion in invasive populations of *Geranium carolinianum* (Geraniaceae). *Heredity,* **112,** 497 - 507.

Skálová, H., Havlíčková, V. & Pyšek, P. (2012) Seedling traits, plasticity and local differentiation as strategies of invasive species of *Impatiens* in central Europe. *Annals of Botany,* **110,** 1429-1438.

Skálová, H., Jarošík, V., Dvořáčková, Ś. & Pyšek, P. (2013) Effect of intra- and inter-specific competition on the performance of native and invasive species of Impatiens under varying levels of shade and moisture. *PloS One,* **8,** 1.

Skálová, H., Moravcová, L. & Pyšek, P. (2011) Germination dynamics and seedling frost resistance of invasive and native *Impatiens* species reflect local climatic conditions. *Perspectives in Plant Ecology, Evolution and Systematics,* **13,** 173-180.

Theoharides, K. A. & Dukes, J. S. (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist,* **176,** 256-273.

Thompson, B. K., Weiner, J. & Warwick, S. I. (1991) Size-dependent reproductive output in agricultural weeds. *Canadian Journal of Botany,* **69,** 442-446.

Tinchý, J. (1997) Changes in forest vegetation on Ondrejník permanent plot after thirty years. *Lesnictví-Forestry,* **43,** 363-373.

Valentine, D. H. (1978) The pollination of introduced species, with special reference to the British Isles and the genus *Impatiens*. *The Pollination of Flowers by Insects* (ed A. J. Richards), pp. 117-134. Academic Press, London.

Valladares, F., Balaguer, L., Martinez-Ferri, E., Perez-Corona, E. & Manrique, E. (2002) Plasticity, instability and canalization: is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? *New Phytologist,* **156,** 457-467.

van Kleunen, M., Johnson, S. D. & Fischer, M. (2007) Predicting naturalization of southern African Iridaceae in other regions. *Journal of Applied Ecology,* **44,** 594-603.

van Kleunen, M., Schlaepfer, D. R., Glaettli, M. & Fischer, M. (2011) Preadapted for invasiveness: do species traits or their plastic response to shading differ between invasive and non-invasive plant species in their native range? *Journal of Biogeography,* **38,** 1294-1304.

Van Kleunen, M., Weber, E. & Fischer, M. (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters,* **13,** 235-245.

Vendramini, F., Díaz, S., Gurvich, D. E., Wilson, P. J., Thompson, K. & Hodgson, J. G. (2002) Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytologist,* **154,** 147-157.

Vervoort, A., Cawoy, V. & Jacquemart, A. L. (2011) Comparative reproductive biology in co-occurring invasive and native *Impatiens* species. *International Journal of Plant Sciences,* **172,** 366-377.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos,* **116,** 882-892.

Vitousek, P. M. (1986) Biological invasions and ecosystem properties: can species make a difference? *Ecology of Biological Invasions of North America and Hawaii* (eds H. A. Mooney & J. Drake), pp. 163–176. Springer, New York.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L. & Westbrooks, R. (1996) Biological invasions and global environmental change. *American Scientist,* **84,** 468-487.

Walker, N. F., Hulme, P. E. & Hoelzel, A. R. (2009) Population genetics of an invasive riparian species, *Impatiens glandulifera*. *Plant Ecology,* **203,** 243-252.

Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil,* **199,** 213-227.

Westoby, M. & Wright, I. J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution,* **21,** 261-268.

Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology,* **77,** 1661-1666.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M. L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature,* **428,** 821-7.

Wulff, R. D. (1986) Seed size variation in *Desmodium paniculatum*: I. Factors affecting seed size. *Journal of Ecology***, 74**, 87-97.

Zybartaite, L., Zukauskiene, J., Jodinskiene, M., Janssens, S. B., Paulauskas, A. & Kupcinskiene, E. (2011) RAPD analysis of genetic diversity among Lithuanian populations of *Impatiens glandulifera*. *Žemdirbystė= Agriculture,* **98,** 391-398.

Paper I

Paper II

Paper III

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Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr.	Winter survival strategies of the Willow tit *Parus*

		philos Zoology	*montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr.	The plant cover of the boreal uplands of Central

		philos Botany	Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great

			Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient	Eevalution of rotifer *Brachionus plicatilis* quality in

		Bothany	early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro

1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient	The Cuckoo (*Cuculus canorus*) and its host: adaptions

		Zoology	and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears

2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins

2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine

			microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d	*Arabidopsis thaliana* Responses to Aphid

		Bilogy	Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments -Focus on formulated diets
2010	Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	ph.d Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	ph.d Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans

2010	Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	ph.d Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in *Arabidopsis thaliana*
2011	Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	ph.d Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	ph.d Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	ph.d Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	ph.d Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	ph.d Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	ph.d Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	ph.d Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	ph.d Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	ph.d Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	ph.d Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	ph.d Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	ph.d Biology	Theoretical and empirical approaches to studying foraging decisions: the past and future of behavioural

			ecology
2012	Aleksander Handå	ph.d Biology	Cultivation of mussels (*Mytilus edulis*):Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	ph.d Biology	Reproductive and migratory challenges inflicted on migrant brown trour (*Salmo trutta* L) in a heavily modified river
2012	Jisca Huisman	ph.d Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	ph.d Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	ph.d Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	ph.d Biology.	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	ph.d Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos.	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	ph.d Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	ph.d Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	ph.d Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	ph.d Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	ph.d Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	ph.d Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	ph.d Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	ph.d Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	ph.d Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	ph.d Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	ph.d Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia

2013	Anders Foldvik	ph.d Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	ph.d Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	ph.d Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Ane Kjersti Vie	ph.d Biology	Molecular and functional characterisation of the IDA family of signalling peptides in ***Arabidopsis thaliana***
2014	Jannik Schultner	ph.d Biology	***Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird***
2014	Craig Ryan Jackson	ph.d Biology	Factors influencing African wild dog ***(Lycaon pictus***) habitat selection and ranging behaviour: conservation and management implications
2014	Michael Puffer	ph.d Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar L.*)"
2014	Gundula S. Bartzke	ph.d Biology	Effects of power lines on moose ***(Alces alces)*** habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	ph.d Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	ph.d Biology	The parasite ***Syngamus trachea*** in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	ph.d Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2
2014	Espen Lie Dahl	ph.d Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	ph.d Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity