Henna Piha

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Impacts of Agriculture on Amphibians at Multiple Scales

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Academic dissertation

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I Teplitsky C, Piha H, Laurila A, Merilä J. 2005. Common pesticide increases costs of antipredator defenses in *Rana temporaria* tadpoles. Environmental Science & Technology 39:6079-6085.

II Piha H, Laurila A, Merilä J. Pesticide effects on tadpoles: interactions with predation risk and competition, and the importance of compensatory growth. Manuscript.

III Piha H, Pekkonen M, Merilä J. 2006. Morphological abnormalities in amphibians in agricultural habitats: a case study of the common frog *Rana temporaria*. Copeia, in press.

IV Piha H, Luoto M, Sterner M, Merilä J. Amphibian occurrence in human-impacted landscapes is influenced by current-day and historic landscape characteristics. Manuscript.

V Piha H, Luoto M, Piha M, Merilä J. 2006. Anuran abundance and persistence in agricultural landscapes during a climatic extreme. Global Change Biology 12:1-12.

Contributions

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Data collection	CT	HP	HP, MPe	JM, MS	HP
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Abstract

Agriculture-mediated habitat loss and degradation together with climate change are among the greatest global threats to species, communities, and ecosystem functioning. During the last century, more than 50% of the world's wetlands have been lost and agricultural activities have subjected wetland species to increased isolation and decreased quality of habitats. Likewise, as a part of agricultural intensification, the use of pesticides has increased notably, and pesticide residues occur frequently in wetlands making the exposure of wetland organisms to pesticides highly probable. In this thesis, a set of ecotoxicological and landscape ecological studies were carried out to investigate pesticide-effects on tadpoles, and species-habitat relationships of amphibians in agricultural landscapes. The results show that the fitness of *R. temporaria* tadpoles can be negatively affected by sublethal pesticide concentrations, and that pesticides may increase the costs of response to natural environmental stressors. However, tadpoles may also be able to compensate for some of the negative effects of pesticides. The results further demonstrate that both historic and current-day agricultural land use can negatively impact amphibians, but that in some cases the costs of living in agricultural habitats may only become apparent when amphibians face other environmental stressors, such as drought. Habitat heterogeneity may, however, increase the persistence of amphibians in agricultural landscapes. Hence, the results suggest that amphibians are likely to be affected by agricultural processes that operate at several spatial and temporal scales, and that it is probable that various processes related to current-day agriculture will affect both larval and adult amphibians. The results imply that maintaining dense wetland patterns could enhance persistence of amphibian populations in agricultural habitats, and indicate that heterogeneous landscapes may lower the risk of regional amphibian population declines under extreme weather perturbations.

Contents

Summary

1. Introduction

The expansion and intensification of agricultural land use during the last century are among the most predominant human-induced changes in the global environment (Matson et al. 1997, Tilman et al. 2002, Green et al. 2005). Conversion of natural habitats to croplands and permanent pastures has reduced the extent of natural habitats on agriculturally usable land by more than 50% (Green et al. 2005). Currently agriculture represents the major form of land use throughout most of Europe and North America, where agricultural production and productivity have intensified rapidly over the past 60 years particularly due to increased mechanization, irrigation and agrochemical use (Matson et al. 1997, Krebs et al. 1999, Green et al. 2005). Despite this general trend, considerable variation in the intensity of agriculture exists among European countries. Agricultural intensification is generally higher in European Union (EU) member countries than in non-EU member countries mostly due to the Common Agricultural Policy (CAP), which is a price-support policy that subsidizes production and keeps prices artificially high (Krebs et al. 1999, Donald et al. 2001). In Finland (EU-member since 1995), only 7% of the land is covered by croplands. However, in the main agricultural regions of southern and western Finland, croplands cover roughly 30% of the land (Pitkänen & Tiainen 2000). Finnish agriculture has intensified in accordance with other EU-countries, major changes including decreased mixed farming and dairy farming, increased farm sizes, intensified land use, loss of meadows, and increased agrochemical use (Pitkänen & Tiainen 2000, Luoto et al. 2003; Fig. 1).

Figure 1. Trends in the total pesticide sales in Finland (Evira 2006). AI = active ingredients.

Although modern-day agriculture has enabled the feeding of the world's growing population, concerns have risen over its sustainability and environmental consequences (Matson et al. 1997, Krebs et al. 1999, Tilman et al. 2002, Green et al. 2005). Expansion of agricultural land has caused extensive habitat loss and degradation, which are among the greatest current and future threats to biodiversity (Sala et al. 2000, Dirzo & Raven 2003). Agricultural intensification has led to widespread farmland biodiversity losses in temperate areas (Krebs et al. 1999, Donald et al. 2001, Benton et al. 2003), and deterioration in soil, water and air quality (Stoate et al. 2001, Tilman et al. 2002). Farming is already the greatest extinction risk to birds and during the next 50 years global agricultural expansion is predicted to cause unprecedented ecosystem simplification, loss of ecosystem services, and species extinctions (Tilman et al. 2001, Green et al. 2005). Additionally, the negative impacts of modern-day agriculture are likely to increase in combination with climate change (Travis 2000, Opdam & Wascher 2004). In the following, I shall focus on three ecologically important aspects of agriculture: (1) the impacts of agricultural expansion on landscape characteristics and different taxa (including non-farmland species), (2) the impacts of agricultural intensification, which chiefly affect farmland species, but can also be far-reaching (e.g. chemicalisation effects), and (3) the combined effects of modern-day agriculture and climate change.

1.1. Expansion of agriculture

The expansion of farmland areas has caused destruction and loss of natural habitats (e.g. wetlands, temperate grasslands, forests) with detrimental impacts on many species (e.g. Bakker & Berendse 1999, Trzcinski et al. 1999, Lienert et al. 2002). Currently wetlands are among the most threatened ecosystems of the world, their total area having declined by more than 50% in Europe and North America during the last century largely due to agricultural expansion (OECD 1996, Zedler & Kercher 2005). The domination of agricultural land in relation to other habitat types means that in agriculture-dominated areas, all other habitats may be embedded in agricultural land, thereupon increasing fragmentation of natural habitats (i.e. loss of habitat leading to a reduction in patch size and increased patch isolation; Andrén 1994) and decreasing habitat quality (e.g. Brinson & Alvarez 2002, McCauley & Jenkins 2005). In smaller and more isolated habitat fragments, species are more prone to local extinctions and population declines than in less fragmented habitats as a consequence of diminished population sizes and reduced colonization and immigration rates (Andrén 1994, Fahrig 2003, Ewers & Didham 2006). For instance, increased isolation caused by agricultural expansion has resulted in the decreased abundance and species richness of flower-visiting bees, and in impaired plant-pollinator interactions (Steffan-Dewenter & Tscharntke 1999), whereas agriculture-mediated forest fragmentation has impacted negatively the occurrence and reproductive success of forest birds (Åberg et al. 1995, Bayne & Hobson 1997). Habitat loss and fragmentation can also affect species through increased edge effects (Fagan et al. 1999, Ries et al. 2004), changes in the microclimate (Saunders et al. 1991), and decreased genetic variation (Young et al. 1996), the latter being observed for example with common frog *Rana temporaria* populations in areas of intensive agriculture (Johansson et al. 2005). Additionally, habitat loss may influence the potential of populations to adapt in response to environmental degradation (Stockwell et al. 2003), and make them more sensitive to other environmental stressors, such as climate change (Travis 2000, Opdam & Wascher 2004).

Many of the negative impacts of modern-day agriculture are related to its effects on matrix quality (i.e. the landscape surrounding suitable habitat patches), particularly the heterogeneity of the matrix (Benton et al. 2003, Opdam & Wascher 2004, Donald & Evans 2006). Matrix quality can be extremely important in determining population dynamics and ecosystem functioning in fragmented landscapes (Fahrig 2001, Vandermeer & Carvajal 2001). It can affect the ability of species to attain resources, their movement and dispersal abilities, and the strength of edge effects, and hence, may in some decrease the negative impacts of fragmentation (Tscharntke et al. 2002, Donald & Evans 2006, Ewers & Didham 2006). In areas of intensive agriculture, landscape heterogeneity has benefited various plant and animal species (e.g. Weibull et al. 2000, Benton et al. 2003, Johansson et al. 2005, Roschewitz et al. 2005). Likewise, heterogeneity among agricultural habitats (i.e. between and within fields) can be important for the maintenance of biodiversity in farmland ecosystems (Robinson & Sutherland 2002, Benton et al. 2003, Donald & Evans 2006), but it is threatened more by the intensification than the expansion of agriculture, as will be discussed next.

1.2. Intensification of agriculture

Agricultural intensification includes various spatial and temporal processes, which aim at increasing crop yields per unit area, but which have increased the homogeneity of agricultural habitats, and caused increased soil erosion, and water and air pollution (Stoate et al. 2001, Benton et al. 2003; Table 1). Negative impacts of agricultural intensification have been demonstrated in many species (Table 1), most of all in farmland birds, which are by far the most studied taxa (reviews in Stoate et al. 2001, Robinson & Sutherland 2002, Benton et al. 2003, Newton 2004). The impacts of agricultural intensification are complex and often difficult to identify, as the different processes can interact and affect organisms both directly and indirectly (Robinson & Sutherland 2002, Benton et al. 2003). The main effects of agricultural intensification on farmland species can be coarsely divided into two groups: those resulting from changes in the availability and quality of breeding and foraging habitats, and those resulting from changes in farmland communities (e.g. Krebs et al. 1999, Donald et al. 2001, Newton 2004; Box 1).

1.3. Agriculture and climate change

Although the impacts of agricultural expansion and intensification on species extend far beyond farmland areas, a key driving force of species' distributions at large biogeographical scales is climate. Human-induced climate change (caused by increased concentrations of greenhouse gases) involves increases in the mean global temperature, changes in the distribution and frequency of precipitation, and increases in the frequency of extreme climatic events, such as droughts and floods (Easterling et al. 2000, Hughes 2000). Global warming has been related to alterations in the distribution and phenology of various taxa, and to changes in the composition and interactions within communities (Hughes 2000, Walther et al. 2002, Parmesan & Yohe 2003, Root

Table 1. Consequences and effects of different processes of agricultural intensification on habitats and species (classification of processes adapted from Benton et al. 2003).

Process	Consequence for agricultural habitats	Effects on species
Farm unit consolidation and specialization	Domination of fewer larger farm units and larger contiguous areas under common management systems and/or crop rotations	Negative associations with habitat availability and density of several farmland bird species (1, 2)
Simplified crop rotations	Larger blocks of land under the same agriculturally productive management at any given time and for longer periods	Negative associations with bird distributions (3)
Removal of uncultivated areas	Loss of semi-natural habitat features, such as ponds, non-cropped field margins and scrub	Declines of bird species (4), arthropods (5, 6), weed diversity (7), and amphibians (8)
Mechanization	More uniform swards, and more fields in the same management state at any one time, stubbles available for only short periods	Declines of various bird species (9, 10)
Grassland improvement	Reduction in species diversity by killing weeds and favoring competitive grass species through drainage and fertilizer use	Negative impacts on the diversity and abundance of birds (3, 11), dung beetles (12), true bugs (13), and bumblebees (14)
Increased agrochemical use	Increased uniformity of establishment and growth, reduced species and structural diversity of vegetation, pollution of soil, air, and ground and surface waters	Negative effects on birds (10), butterflies (15), arthropod communities (12, 16-18), amphibians (19), and wood mice (20)
Increased drainage and irrigation	More uniform establishment and crop growth, increased erosion, decreased water supplies	Negative impacts on bird and invertebrate abundances (3, 10, 21), potential threat to bumblebees (22), and amphibians (23)

Cited references:

1. Blanco et al. 1998
2. Robinson & Sutherland 2002
3. Atkinson et al. 2002
4. Peach et al. 2004
5. Dennis et al. 1994
6. Holland & Fahrig 2000
7. De Snoo 1999
8. Vos & Stumpel 1995
9. Chamberlain et al. 2000
10. Newton 2004
11. Vickery et al. 2001
12. Hutton & Giller 2003
13. Di Giulio et al. 2001
14. Croxton et al. 2002
15. Longley & Sotherton 1997
16. Chiverton & Sotherton 1991
17. Sotherton 1998
18. Haughton et al. 1999
19. Davidson 2004
20. Tew et al. 1992
21. Stoate et al. 2001
22. Diekotter et al. 2006
23. Johansson et al. 2005

Box 1. Examples of the main ways in which agricultural intensification can affect species. Group 1 = changes in habitat availability and quality; Group 2 = changes in farmland community structure and functioning.

Group 1: Loss of semi-natural habitats
The loss of semi-natural habitats has had wide-ranging impacts on terrestrial and aquatic species alike. The removal of field boundaries and uncultivated areas, for instance, has led to the loss of suitable terrestrial breeding and foraging habitats for many species, whereas the drainage and filling of ponds has significantly decreased the availability of small wetlands (e.g. Beebee 1983), which often support diverse aquatic communities (Oertli et al. 2002, Nicolet et al. 2004, Williams et al. 2004) and are important habitats for many farmland birds (Newton 2004, Bradbury & Kirby 2006). The remaining aquatic habitats are also likely to experience a decrease in quality caused by agricultural intensification (e.g. grazing disturbance, nutrient and pesticide runoff; Knutson et al. 2004, Declerck et al. 2006), which may reduce their value for farmland diversity (Bradbury & Kirby 2006) For discussion on pesticide-effects in aquatic habitats see 3.1.

Group 2: Pesticide-mediated changes in food webs
A classical example of agriculture-mediated changes in food webs is the impact of pesticide-use on partridge populations in the U.K. (Green 1984, Rands 1985). It was shown that the use of herbicides decreased the abundance of weeds, which resulted in decreased arthropod abundances, which in return caused impoverished food supplies for partridge chicks (Chiverton & Sotherton 1991). These changes led to increased chick mortality and consequent population declines (Green 1984, Rands 1985, Potts & Aebischer 1995). The use of insecticides has also been shown to depress breeding productivity of birds by decreasing insect food abundances (Hart et al. 2006), and in Scotland, a link between arthropod abundances, farmland birds and agricultural practices has recently been clearly shown (Benton et al. 2002). For discussion on pesticide-effects on the functioning of aquatic communities see 3.2.

et al. 2003), whereas climatic extremes have been shown to cause synchronized population crashes and extinctions (e.g. Thomas et al. 1996, Sutcliffe et al. 1997, Hawkins & Holyoak 1998). The impact of climate change on the abundance and persistence of species can be affected by habitat loss. Firstly, the shifting of species ranges in response to climate change may be blocked in areas where the degree of habitat fragmentation is below the level required for population persistence, and secondly, the increased frequency of large-scale disturbances caused by climatic extremes may cause increasing gaps and an overall contraction of distribution ranges (Warren et al. 2001, Opdam & Wascher 2004). Habitat heterogeneity can to increase population persistence under variable climatic conditions (Weiss et al. 1988, Kindvall 1996, McLaughlin et al. 2002), but as modern-day agriculture causes both habitat loss and homogenization, it is likely that in agricultural landscapes, species may be particularly sensitive to climate change (Travis 2002, Donald & Evans 2006).

1.4. Amphibians and agriculture

In recent studies on the effects of agricultural intensification on biodiversity, amphibians have usually been brushed aside (e.g. Stoate et al. 2001, Robinson & Sutherland 2002, Hole et al. 2005). This is surprising, as among amphibian researchers, various processes related to agricultural intensification are regarded as major threats to amphibian individuals and populations (e.g. Joly et al. 2001, Linder et al. 2003, Semlitsch 2003, Knutson et al. 2004, Relyea et al. 2005), and to be partly responsible for global amphibian population declines (Box 2). In the following, I shall illustrate how and why amphibians may be affected by modern-day agriculture, and some of the approaches to studying the impacts of agricultural intensification on amphibians. Amphibians are an extremely diverse vertebrate class with large variation in physiological, behavioral, morphological and ecological characteristics (Feder & Burggren 1992). In the following, when speaking of amphibians, I refer to species which employ a general life history strategy entailing the use of aquatic habitats for reproduction and larval development, and terrestrial habitats for growth to maturation and dispersal. I also restrict my discussion primarily to pond-breeding species (i.e. amphibians which use lentic aquatic habitats such as pools, ponds, lakes, and marshes for breeding) living in temperate regions, because all my work has been conducted with such species, and they are the most common type of amphibians in Europe and North America with important roles in ecosystems (Box 3).

Pond-breeding amphibians require both aquatic and terrestrial habitats, and are hence subject to alterations in the availability and/or quality of either habitat type (Semlitsch 2000). Consequently, they are likely sensitive to habitat loss caused by agricultural expansion (Laan & Verboom 1990, Hecnar & M'Closkey 1998, Houlahan & Findlay 2003), to increased isolation of breeding and foraging habitats (increased survival risks related to longer migrations and distances to neighboring source populations in a possibly hostile matrix; e.g. Gibbs 1993, Joly et al. 2001, Rothermel & Semlitsch 2002), and to the decreased quality of breeding sites (e.g. Cooke 1981, Knutson et al. 2004, Declerck et al. 2006). Additionally, the reduced amount of ditches caused by increased subsurface drainage can hinder amphibian movement (Reh & Seitz 1990, Pope et al. 2000, Mazerolle 2004).

Box 2. Global amphibian population declines.

Currently approximately one third of the world's amphibian species are threatened and at least 43% of all species have declined (Stuart et al. 2004). Habitat loss and degradation are among the greatest threats to many of the declining populations, but additional threats include pesticides and other chemical pollutants, increased UV-B radiation, climate change, introduced predators, diseases, and exploitation (Collins & Storfer 2003, Beebee & Griffiths 2005, Pounds et al. 2006). Additionally, findings of amphibian populations with unexpectedly high incidences of morphological abnormalities have been made particularly in the U.S. (Blaustein & Johnson 2003, Sessions 2003). It is likely that the stressors are not working independently, but interactions amongst them may be the most likely threat to many species (e.g. Kiesecker et al. 2001, Blaustein & Kiesecker 2002, Pounds et al. 2006).

Several intrinsic and extrinsic factors increase the likelihood of amphibians being sensitive to agricultural intensification. Firstly, many amphibian species have strong annual population fluctuations (Pechmann et al. 1991, Meyer et al. 1998, Trenham et al. 2003), high site fidelity (Smith & Green 2005), and relatively weak dispersal abilities (Sinsch 1990, but see Smith & Green 2005), which may make them particularly sensitive to isolation effects. Secondly, they have semi-permeable skins which protect them weakly against contaminants and drying (Feder & Burggren 1992). They are particularly likely to be exposed to pesticides during the aquatic development, as it coincides with the timing of pesticide use. For example, species of the ranid frogs in the U.S. breed sequentially throughout the spring and summer, and breeding periods may extend over periods of many weeks. Hence it is very likely that at least some of the species will be exposed to pesticides (Berrill et al. 1994). Furthermore, because aquatic habitats are the ultimate sinks for most chemical contaminants regardless of their source, aquatic stages of amphibians are likely exposed even if the breeding sites are not situated within agricultural landscapes. However, exposure to pesticides during terrestrial development may likewise pose a threat for amphibians (e.g. Relyea 2005).

1.5. Scales and approaches to studying agricultural impacts on amphibians

The problems and impacts of scale have long been central issues in ecological studies (Wiens 1989, Levin 1992). Each individual and species experiences the environment at a unique range of scales, and different processes are likely to be important on these different scales (Levin 1992). Generally climate is expected to govern organisms' responses at broad biogeographical scales whereas land cover and biotic interactions are considered to dominate at finer spatial resolutions (Parmesan 1996, Pearson et al. 2004, Luoto et al. 2006). Due to this, and because agriculture operates at several spatiotemporal scales, no single measure can explain amphibian responses to agricultural intensification (Burel et al. 2004). Therefore, when studying the impacts of agriculture on amphibians, incorporation of multiple spatial and temporal scales as well as different approaches is necessary.

Box 3. Important ecosystem roles of pond-breeding amphibians (adapted from Petranka & Kennedy 1999, Semlitsch 2003).

Larval anurans (frogs and toads) are both microphagous suspension feeders (consuming e.g. pollen, algae, periphyton, microorganisms, and -zooplankton) and macrophagous predators (consuming e.g. macroinvertebrates, amphibian eggs, hatchlings and tadpoles), whereas larval caudates (salamanders and newts) generally only consume secondary production. Terrestrial adults feed on small invertebrates often not available to other vertebrate groups. Pond-breeding amphibians comprise a large amount of protein biomass that is available in the food chain (e.g. for snakes, birds, and mammals) and serve as nutrient vectors connecting aquatic and terrestrial environments through emigration and immigration processes.

Choice of scale

Firstly, effects of agricultural intensification can be studied at the scale of the individual, population, community or ecosystem. Individual-based studies make possible the investigation of specific mechanisms, whereas studies at the population-level or higher take into account impacts on population dynamics, species-interactions, and ecosystem functioning, which cannot be estimated from individual-based studies. Secondly, it is probable that different developmental stages experience the environment on different scales (Levin 1992), and amphibians with their biphasic lifestyles are a good example of this. Hence, it is likely that different processes of agricultural intensification are important for the aquatic than for the terrestrial life stages (see 1.4.), and this should be acknowledged when planning investigations. Thirdly, the scale-dependence of different agricultural processes (Benton et al. 2003) makes it likely that amphibian populations will be affected by agricultural processes operating at both local and landscape levels. When making choices regarding the levels to study, it is worth remembering that when moving from small scale approaches to large scale approaches (spatial and temporal) one has to trade off the loss of detail for the gain of generality (Levin 1992).

Choice of approach

To study the effects of agricultural intensification on amphibians, it is possible to carry out experimental (manipulative) or observational (mensurative) studies (Hurlbert 1984). Pesticide-effects are often studied using larval amphibians (see 2.1.) and by conducting manipulative experiments. The venue can be laboratory, mesocosm, or field. Laboratory experiments allow the isolation of effects of particular mechanisms, whereas mesocosm and field experiments are subject to environmental variability and are structurally more complex, hence allowing the prediction of effects on natural populations and ecosystem-level features (Kimball & Levin 1985, Skelly & Kiesecker 2001). Laboratory experiments are generally expected to yield the more precise estimates of responses compared to mesocosm and field studies, however, this difference may not always be apparent (Skelly & Kiesecker 2001). Impacts of habitat composition and configuration are generally approached by means of observational studies. The benefit of observational studies is that they have high realism and generality, because they are applied to unmanipulated, real-world systems. However, the results are correlative and cannot be used to distinguish cause from effect (McGarigal & Cushman 2002). Outside of the breeding season, adult amphibians are tedious to study. Hence, most studies investigating amphibian distributions, abundance and diversity are conducted by studying breeding pond assemblages. This enables observations to be made at large scales, but more detailed studies are needed to gain information of e.g. amphibian migration and small-scale habitat characteristics important for the terrestrial stages.

2. Aims of the thesis

The aim of my thesis was to study impacts of agricultural intensification on amphibians at multiple scales. Firstly, by studying common frog *Rana temporaria* tadpoles, I wanted to examine how fenpropimorph, a commonly used morpholine fungicide, may affect the fitness of tadpoles, and their ability to cope with natural stressors (**I-II**; Fig. 2). Secondly, by studying breeding populations of four amphibian species (common frog *Rana temporaria*, moor frog *Rana arvalis*, common toad *Bufo bufo*, smooth newt *Triturus vulgaris*), I wanted to examine which habitat characteristics impact the abundance, distribution and persistence of these species (**IV, V**), and the morphological development of *R. temporaria* tadpoles in agricultural areas (**III**; Fig. 2). Hence, I aimed to understand how processes related to agricultural expansion and intensification may affect both the aquatic and terrestrial stages of amphibians. I studied these issues by applying ecotoxicological (**I-III**) and landscape ecological (**III-V**) approaches, and by conducting laboratory (**I**), outdoor mesocosm (**II**), and observational field studies in southern Finland (**III, V**; Fig. 3) and on the Island of Gotland, Sweden (**IV**; Fig. 3).

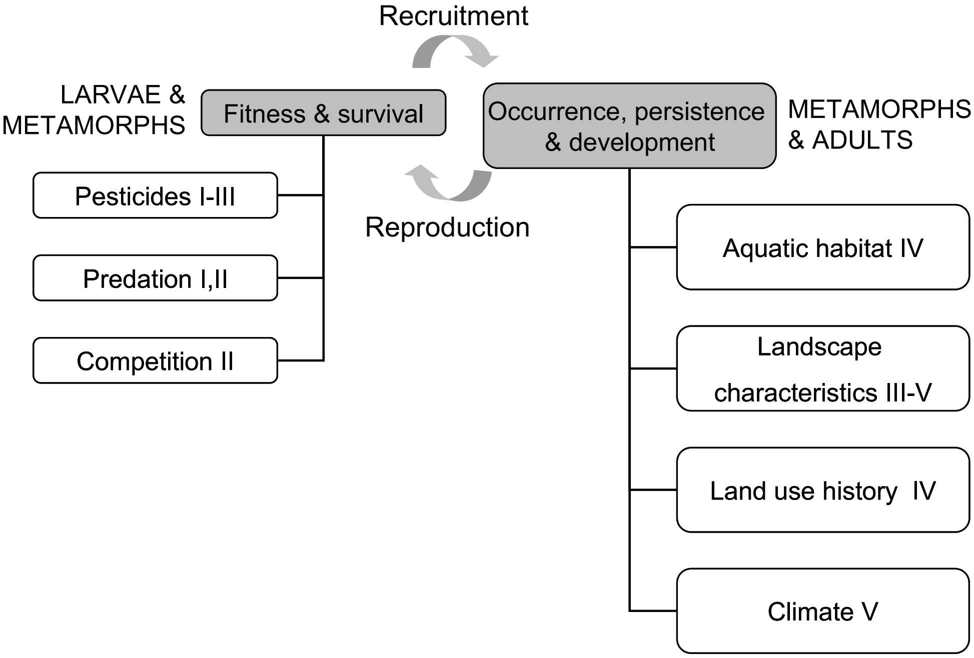

Figure 2. The response variables (gray box), explanatory variables (open box), and amphibian life stages studied in the thesis.

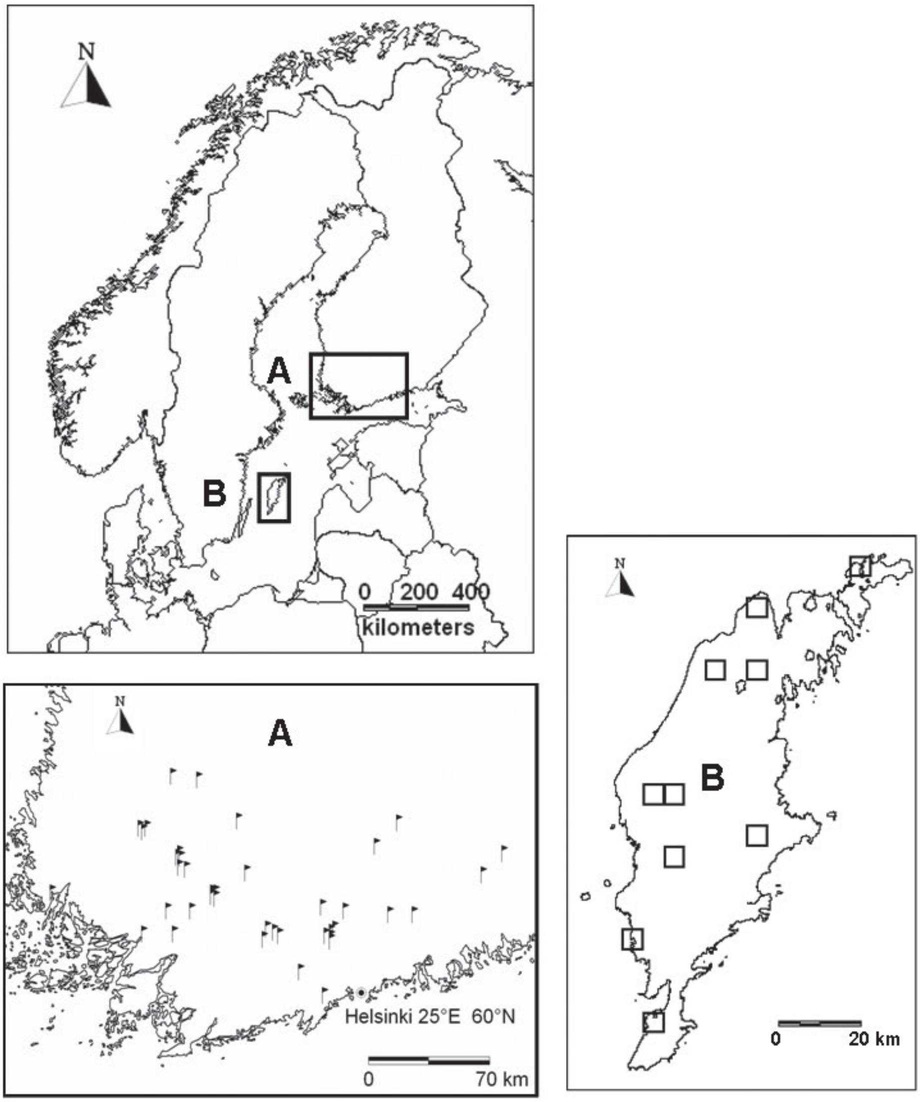

Figure 3. The study areas used in articles III-V and the locations of the study sites. A = southern Finland, B = Swedish island of Gotland.

3. Main results and discussion

The main study questions and main results of the five articles are summarized in Table 2. In the following, I shall discuss these results and their broader significance with respect to published literature.

3.1. Pesticide-effects on aquatic organisms

Organisms living in aquatic habitats are likely exposed to a wide range of contaminants via water, sediment, and food (Farrington 1991). At concentrations occurring in natural habitats, many contaminants are lethal to freshwater organisms, such as fish (Lemly 2002, Hopkins et al. 2004), amphibians (Berrill et al. 1998, Harris et al. 1998a, Boone & James 2003), invertebrates (Schulz & Liess 1999), and microorganisms (DeLorenzo et al. 2001, Hanazato 2001; for a comprehensive database on pesticide toxicity to aquatic species see PAN Pesticides Database http://www.pesticideinfo.org). Long-term exposure to fenpropimorph at concentrations occurring in natural habitats (11 µg/L) was highly lethal to *Rana temporaria* tadpoles (**I**). However, it is likely that tadpoles are not exposed to such high concentrations chronically in nature. Chronic exposure to considerably lower fenpropimorph concentrations (2 µg/L) nevertheless reduced metamorphic size (**I**), and under pulse exposure it slowed the tadpoles' growth and development (**II**). Time to and size at metamorphosis are important fitness characteristics of amphibians, as they are positively correlated to adult growth, survival and reproductive success (Smith 1987, Semlitsch et al. 1988, Berven 1990, Semlitsch & Gibbons 1990, Altwegg & Reyer 2003). Large size at metamorphosis can also benefit physiological and locomotor performance in terrestrial environments (Pough & Kamel 1984, Goater et al. 1993), and high development rates enable tadpoles to metamorphose before habitats dry up (Smith 1983, Newman 1988, Laurila & Kujasalo 1999, Loman 2002), which is a likely threat for tadpoles developing in temporary habitats in agricultural landscapes. These results (**I, II**) together with other amphibian studies showing similar sublethal pesticide-effects (reduced larval growth and development: Berrill et al. 1998, Rohr et al. 2003, Broomhall 2004, Relyea 2004a; increased age and decreased size at metamorphosis: Fioramonti et al. 1997, Bridges 2000, Sullivan & Spence 2003) suggest that current agriculture-related pesticide use can pose a threat to amphibian populations in the wild by decreasing the fitness of individuals.

The negative effects of pesticides on organisms can result from accumulation (Sparling et al. 2001), metabolic changes (e.g. elevated standard metabolic rates; Weber 1996, Rowe et al. 2001), and physiological effects (e.g. immune toxicity; Galloway & Handy 2003, Gendron et al. 2003). Also behavioral changes (activity, predator avoidance, feeding) are caused by many pesticides (Cooke 1971, Weber 1996, Bridges 1997, Berrill et al. 1998). Fenpropimorph affected the behavior of *R. temporaria* tadpoles negatively by decreasing their activity (**I, II**), which likely explains part of the negative effects observed on metamorphic size (**I**). Stressor-effects may not, however, be directly apparent, but be seen as negative carry-over effects at a later stage of development (Bridges 2000, Pahkala et al. 2003, Rohr et al. 2006a). Alternatively, when exposure to a stressor is not chronic, individuals may

Table 2. Summary of the main study questions and results of the five articles included in the thesis.

	Main study questions	**Main results**
I	Are environmentally realistic fenpropimorph (FEN) concentrations harmful to *Rana temporaria* tadpoles?	FEN decreased the tadpoles' activity, growth and development rate. At 11 µg/L, FEN was highly lethal, whereas at 2 µg/L, FEN decreased the size of the metamorphs.
	Does FEN impede inducible responses to predation risk?	FEN did not impede behavioral or morphological responses to predation risk.
	Does FEN increase the costs of responding to predation risk?	At 2 µg/L, the costs of antipredator defenses (decreased size, prolonged development) were higher than in the absence of FEN.
II	Do predation risk and competition alter the effects of FEN on *R. temporaria* tadpoles?	Tadpoles metamorphosed at a smaller size from the high FEN treatment when competition was low, but not at other densities.
	Does FEN impede the inducible responses of tadpoles to predation risk and competition?	FEN impeded the tadpoles from increasing their activity in response to competition under predation risk. Morphological responses were not impeded.
	Does FEN increase the costs of responding to predation risk and competition?	Although FEN had negative synergistic and additive effects with predation risk and competition on tadpoles, by metamorphosis the effects had largely disappeared, likely due to compensatory growth of the tadpoles.
III	Does the abnormality frequency in *R. temporaria* populations differ from the expected background frequency of 0-5% in agricultural areas?	The frequency of morphological abnormalities in metamorphs did not differ from the expected background frequency, abnormalities occurring in only 1.0% of the 4115 studied individuals.
	Does the abnormality frequency differ among different types of agricultural habitats?	No significant differences were observed among the different types of habitats (field, grassland, forest).
IV	How do local habitat, and current-day and historic landscape characteristics explain amphibian occurrence and species richness in agricultural areas of Gotland?	Amphibian occurrence was best explained by local habitat characteristics, however historic landscape characteristics generally explained as much of the variation in response variables as current-day landscape characteristics. Agricultural land use (both current-day and historic) was negatively associated with species' occurrences.
	Are the effects of landscape characteristics in explaining amphibian occurrence scale and/or species dependent?	Species responded rather similarly to different spatial scales of the landscape. The effects of historic landscape characteristics were generally observed at larger spatial scales than those of current-day landscape.
V	Which local, landscape and regional habitat characteristics explain *R. temporaria* abundance in agricultural areas during a normal (2002) vs. a drought year (2003)?	In 2002, abundance was best explained by local habitat characteristics (amount of ditches and ponds). In 2003, regional (water level) and landscape (forests) were positive determinants of abundance, whereas field area (landscape level) correlated negatively.
	What is the role of habitat structure on population persistence during an extreme drought?	The populations decreased less in areas where the change in water levels was smaller and where habitat heterogeneity and coverage of urban areas at the landscape scale were higher.

be able to compensate for the negative effects on growth with compensatory growth (Ali et al. 2003). Compensation of negative pesticide-effects has been shown at the population level (e.g. Forbes et al. 2001, Hooper et al. 2003), however, compensation at the individual level following pesticide exposure has received less attention in amphibian studies. Such a response was present with *R. temporaria* tadpoles, which compensated for the negative effects of fenpropimorph on growth so that by metamorphosis, these effects had mostly disappeared (**II**). These results imply that organisms may be able to compensate for some of the adverse effects of pesticides, and illustrate the importance of taking into account several endpoints for measuring effects of toxicants on the fitness of individuals. However, it should be acknowledged that compensatory growth can also impose costs for organisms, such as adverse effects on later growth, reproduction or survival (Metcalfe & Monaghan 2001, Ali et al. 2003, Mangel & Munch 2005).

Contaminants can also cause abnormal development in organisms. In laboratory experiments, sublethal levels of various pesticides have caused developmental abnormalities (e.g. visceral, mouth, eye and limb deformities) in embryos and larval amphibians (e.g. Alvarez et al. 1995, Harris et al. 1998a, Bridges 2000, Greulich & Pflugmacher 2003, Rohr et al. 2003), and multiple mechanisms exist whereby pesticides may elicit demasculinizing effects in non-target organisms (LeBlanc et al. 1997, see Hayes et al. 2002). Increased frequencies of developmental abnormalities have been observed in amphibians in agricultural habitats and in relation to agricultural land use in the U.S., Canada, and Britain (Cooke 1981, Ouellet et al. 1997, Bishop et al. 1999, Hayes et al. 2002, Taylor et al. 2005). In Europe, recent knowledge of the incidence of developmental abnormalities is largely lacking (Ouellet 2000), and no large-scale studies on the occurrence of amphibian abnormalities in agricultural landscapes had previous to study **III** been carried out. In the agricultural habitats of southern Finland, abnormalities were not exceptionally high in *R. temporaria* metamorphs, abnormalities occurring in only 1% of the studied individuals (Table 2, **III**). These results together with reports of low abnormality frequencies in some farmland areas in the U.S. (Harris et al. 1998a, 1998b, Gillilland et al. 2001) suggest that it is perhaps too early to say that amphibians would generally be at greater risk of obtaining abnormalities in agricultural habitats than in other types of landscapes. More studies at large geographical and longer temporal scales combined with water sample analyses should be carried out in agricultural habitats for a comprehensive understanding of this phenomenon. Meanwhile, it is important to remember that the negative effects of pesticides can be manifested through other paths (sublethal and lethal, direct and indirect; discussed in 3.1. and 3.2.), and hence developmental abnormalities should not be used as the sole indicators of pesticide-effects. It is also probable that other factors, such as *Ribeiroia* parasites (Johnson et al. 2002, 2003) or UV-B radiation (Pahkala et al. 2001, Ankley et al. 2002) are responsible for some of the cases where increased frequencies of abnormalities have been observed.

A major challenge in estimating the impacts of pesticides on organisms is that the effects depend on various factors such as chemical characteristics (dose; **I, II,** mode of action), characteristics of the organisms (species, life stage, size), and context (other environmental factors; **I, II**), see reviews (in DeLorenzo et al. 2001, Hanazato 2001, Rohr et al. 2006b). The combined effects of pesticides and other contaminants (MIX), or pesticides and biotic stressors (BIO) to species of aquatic communities may be additive (MIX: Fairchild et al. 1994, Relyea 2004a; BIO: Sibly et al. 2000, **I, II**), antagonistic (MIX: Hoagland et al. 1993; BIO: Sibly et al. 2000, Hooper et al. 2003), or synergistic (MIX: Howe et al. 1988, Anderson & Lydy 2002; BIO: Hanazato 1999, Relyea & Mills 2001, Kiesecker 2002, Relyea 2003a, **I, II**). From this follows that in nature, contaminants may lead to complex indirect effects, which modify species interactions and population, community and ecosystem functioning (Hanazato 2001, Fleeger et al. 2003, Rohr et al. 2006b, see also 1.2.). As importantly, contaminants may interfere with the ability of organisms to adapt to natural variations in their environment (e.g. Barry 2000) which may lead to population declines and altered community functioning (alike described above). In the following, I shall discuss possible effects of pesticide-exposure on the ability of individuals to cope with predation and competition.

3.2. Pesticides and biotic stressors

Larval anurans often develop in environments where the levels of predation and competition are variable and unpredictable (e.g. Wilbur 1980). Under such circumstances, phenotypically plastic responses in behavior and morphology protect organisms against biotic stressors and enhance their fitness (Tollrian & Harvell 1999, Box 4). Pesticides may, however, alter the effects of predation and competition on organisms and vice versa, or organisms' ability to respond to these stressors. Fenpropimorph decreased the activity of *R. temporaria* tadpoles (**I, II**), and hence did not impede their behavioral response to predation stress (Box 4). However, fenpropimorph impeded the tadpoles from responding to competition in an adaptive way, as they were unable to increase activity as a response to increasing competition when experiencing predation risk (Box 4, **II**). Hence, synergistic negative effects on adaptive plastic responses were observed.

The effects of pesticides on phenotypic plasticity have thus far remained largely unstudied. However, the few studies investigating pesticide-effects on phenotypic plasticity have shown that pesticides can inhibit the development of neckteeth in *Daphnia* in response to predation threat (Barry 2000). Additionally, the costs of responding to biotic stressors may increase under pesticide stress (Hanazato 1999, Barry 2000, Hanazato 2001). Also fenpropimorph increased the costs of responding to predation risk, which could be seen as a decreased relative size of the tadpoles and increased time to metamorphosis (**I**). These results imply that in contaminated habitats organisms may have lowered fitness due to impeded adaptive responses to environmental factors, or to increased costs of responding to the factors. Considering that pesticides may also increase susceptibility to predation (Cooke 1971, Verrell 2000, Schulz & Dabrowski 2001, Broomhall 2004) and that the lethality of pesticides may increase when combined with predation risk (Relyea & Mills 2001, Relyea 2003a) it is presumable that pesticides can pose a threat to amphibians also at the population level (Sih et al. 2004a, 2004b, but see Schmidt 2004). Nonetheless, it should be remembered that at the community level, interactions between pesticides and biotic factors may result in complex changes in

Box 4. Induced responses of tadpoles to predation and competition.

Typical responses of tadpoles to predation risk are altered behavior (decreased activity, increased hiding, altered microhabitat use;1-4, **I, II**) and/or morphology (development of relatively small bodies and deep tails;5-7, **I, II**).These responses increase the likelihood of survival in predator-environments (e.g. improved escape ability; 8, decreased encounter rates; 1) but may include costs, such as decreased growth and development rate (2, 6, 9-13, **I, II**), delayed maturity or reduced fecundity (14), increased energetic swimming costs (15), and lowered survival in the absence of predation (8). The costs may arise from various factors, such as maintenance and production of induced defenses (16), and shifts in allocation of time and energy (13). Tadpoles can modify their responses according to the diet of the predators (stronger responses when conspecifics killed; 17, 18), and to the amount of prey eaten or number and/or type of predators present (19-22). Their responses can also depend on their development stage (23), and their phenotypic strategy can change over ontogeny and be reversible in response to predator presence and absence (7).

Competition generally induces increased activity (3, 24, 25, **II**), which results in more encounters with food and hence results in higher energy gain that translates to higher growth rate and larger size (26). Tadpoles also respond to competition with morphological responses, such as relatively large bodies, wide mouth parts and small tails (27-29, **II**). These plastic responses increase the tadpoles' competitive ability, but may increase their risk of being preyed upon (3, 28). When confronted with predation and competition, organisms generally face a trade-off situation between predator resistance ability and competitive ability (30), as competition and predation often induce traits in opposite directions (28, 31, 32, **II**).

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food resources and predator-prey dynamics (Boone & Semlitsch 2003, Boone et al. 2004, Mills & Semlitsch 2004, Relyea et al. 2005, Rohr & Crumrine 2005) in having positive effects on some species whereas negative on others. Positive effects on tadpoles include predator-release (occurring when predators are more vulnerable to pesticide exposure than tadpoles; Boone & Semlitsch 2003, Mills & Semlitsch 2004, Relyea et al. 2005), and increased food resources (Boone & Semlitsch 2002, Boone et al. 2004). Whereas, by decreasing algal abundance pesticides may exacerbate the effects of competition (Mills & Semlitsch 2004).

3.3. Role of habitat characteristics at multiple scales

Spatial scale

In general, organisms are expected to favor environments in which their survival and reproductive success is maximized. Because the amphibian life history includes aquatic and terrestrial stages, it is not surprising that both local and landscape scale characteristics have been shown to be important determinants of amphibian distributions (e.g. Mazerolle & Villard 1999, Joly et al. 2001, Knutson et al. 2004, Van Buskirk 2005, **IV, V**). In Gotland, in landscapes modified by agriculture, local pond characteristics were stronger determinants of amphibian occurrence and species richness than landscape characteristics (**IV**). Canopy cover of the shoreline was positively associated with the occurrences of *Rana arvalis* and *Triturus vulgaris*, and *R. arvalis* and *Bufo bufo* were more likely to occur in ponds which were small, deep and scarcely vegetated, than in large, shallow, and densely vegetated ponds. The latter relationships likely reflect effects of hydroperiod, the species avoiding habitats which may dry up before the tadpoles have had time to metamorphose. Many amphibian species avoid ponds that contain predatory fish (Kats et al. 1988, Wellborn et al. 1996, Hecnar & M'Closkey 1998). In Gotland, amphibians occurred more likely in ponds where predators (invertebrates and fish) and competitors were present (**IV**), a result which intuitively seems contradictory. However, not all amphibian species avoid habitats with predatory fish (e.g. Laurila & Aho 1997, Laurila 1998), and also other studies have found positive correlations with predator presence and amphibian abundance and diversity (Lehtinen et al. 1999, Babbitt et al. 2003, Van Buskirk 2005). It is likely that these positive correlations reflect the quality of the habitats (Babbitt et al. 2003, Van Buskirk 2005), hence avoiding predation or competition may be less important than finding a pond that fulfills other quality requirements.

For a pond to be occupied by an amphibian, it must be within the limits of a species' dispersal capability. In Finnish agricultural landscapes, *R. temporaria* abundance was positively linked to the number of ditches and area of ponds in the surrounding landscape (**V**), whereas in Gotland, amphibian occurrence and diversity correlated positively with the proportion of wetlands and negatively with the proportion of arable land in the landscape surrounding breeding ponds (**IV**). The positive relations with wetland area likely reflect successful dispersal and migration events between habitats (Cushman 2006), which ensure population persistence irrespective of variation in other environmental factors (Hanski 1998, Joly et al. 2001), but they may additionally arise from enhanced likelihoods of finding compensatory breeding and wintering habitats when traditionally used habitats are dry (Bowne et al. 2006). Parallel positive relations between amphibians and wetland area (Vos & Stumpel 1995, Kolozsvary & Swihart 1999, Joly et al. 2001), and negative ones between arable area (Joly et al. 2001, Beja & Alcazar 2003, Johansson et al. 2005) have been observed in other amphibian studies in farmland areas. These results give reason to believe that amphibian populations may be adversely affected by the expansion and intensification of agriculture, particularly by the loss of aquatic habitats, and that in addition to preserving terrestrial connectivity (Cushman 2006) also dense wetland patterns should be remained to ensure regional viability of amphibian populations.

Temporal scale

Forests are often essential determinants of amphibian distributions in agriculture-dominated areas (Laan & Verboom 1990, Joly et al. 2001, Guerry & Hunter 2002, Porej et al. 2004), but this was not found for amphibian occurrence in Gotland (**IV**) or *R. temporaria* abundance in Finland during normal weather conditions (**V**). However, after a severe drought (and consequent population crashes), *R. temporaria* populations were more abundant in areas where the neighboring landscape had more forests (**V**). These results suggest that the importance of forests for amphibians can be context dependent and vary according to climatic conditions. It is possible that during the drought the agricultural landscape became more hostile, and the forests increased the migratory success of adults (as they have been shown for juvenile amphibians; Rothermel 2004), and provided protection against drying. Similarly, the area of cultivated land was negatively associated with amphibian abundance only after the drought (**V**). Finnish agricultural landscape is a mosaic of forests and cultivated habitats, which may explain why the positive associations with forest area and negative ones with agricultural land arose only after the drought.

R. temporaria populations persisted during drought better in more heterogeneous landscapes (**V**). Habitat heterogeneity has been shown to promote diversity, reduce the extinction risk of populations in fragmented habitats (Ricketts 2001), and buffer against the impacts of agricultural intensification (Donald & Evans 2006, see 1.1.). Our study suggests that heterogeneity of agricultural landscapes may furthermore enhance population persistence during climatic extremes (**V**). Our findings support the view that habitat heterogeneity can dampen the effects of environmental stochasticity by decreasing the synchrony of population fluctuations (Kindvall 1996, Sutcliffe et al. 1997, McLaughlin et al. 2002), and hence protect against variable climatic conditions and enhance the maintenance of populations (Ehrlich & Murphy 1987, Kindvall 1996, Weiss et al. 1998). This can have significant ramifications as extreme events are likely to occur more frequently as a part of the ongoing climate change (Easterling et al. 2000, IPCC 2001).

To better understand present species distributions in relation to land use parameters, knowledge of past habitat characteristics can be central (Swetnam et al. 1999, Lunt & Spooner 2005). Historical land use may affect the quality of present-day habitats (e.g. soil characteristics; Honnay et al. 1999, Verheyen et al. 1999), and present-day species distributions may reflect past habitat circumstances if populations have not yet responded to habitat loss (a time lag in their responses; Tilman et al. 1994, Kareiva & Wennergren 1995). This may lead to the situation where species are present in habitats from which they will go extinct in the future (e.g. Brooks et al. 1999, Lindborg & Eriksson 2004, Helm et al. 2006). In Gotland, amphibian occurrences were negatively associated with the historic proportion of arable land in the surrounding landscape and positively with historic forest area (**IV**). Although the amount of unexplained variation in this study was high, the results indicate that areas with long agricultural histories may be of poorer quality for amphibians, and that agricultural expansion has negatively impacted amphibian distributions in Gotland. Additionally the results suggest that the distribution patterns of amphibian species are likely to reflect an interplay between local and regional habitat quality and historical land use.

4. Conclusions

Agricultural intensification has been estimated to be one of the greatest threats to biodiversity. In this thesis, I showed that current-day agriculture can impact amphibians in many, often negative ways. Pesticide exposure decreased the survival, and impeded the adaptive responses of *Rana temporaria* tadpoles to biotic stressors and increased the costs related to these responses, hence decreasing their fitness. Decreased fitness and survival of tadpoles may affect the viability of amphibian populations negatively, and for *R. temporaria*, larval survival in particular has been estimated to have a strong influence on population dynamics (Biek et al. 2002). However, as pointed out by e.g. Forbes et al. (2001) and Schmidt (2004), the link between individual-level and population-level responses is not straightforward, because population-level effects may be influenced by density-dependent, compensatory responses. Keeping this in mind, I argue that the results of my thesis show that pesticides can interfere with key processes in aquatic communities, and affect the quality of surviving individuals. How pesticide exposed juveniles cope during their adulthood and whether e.g. negative carryover effects on survival and reproductive success can be seen at later life stages, would need further investigations.

I also demonstrated that agricultural intensification may negatively impact the occurrence of amphibians and decrease their ability to persist during varying climatic conditions. The results suggest that in some cases, the costs of living in areas of intensive agriculture may become apparent only when other environmental stressors are present. Maintaining heterogeneous landscapes with enough wetlands would seem to benefit amphibians in agricultural landscapes. Many countries have adapted agri-environment schemes, which aim at reducing agrochemical emissions, restoring landscapes and protecting biodiversity (Klein & Sutherland 2003), and e.g. organic farming and set-aside lands have been shown to benefit biodiversity in many areas (Van Buskirk & Willi 2004, Hole et al. 2005). My results insinuate that these farming practices could benefit amphibians as well, and that their impacts on amphibians would be an area of fruitful future investigations.

The results obtained in my thesis imply that for amphibians in agricultural habitats, it is essential that there exists enough wetlands adjacent to the breeding sites. Recently it was shown that pond quality does not explain the absence of *R. temporaria* and *Rana arvalis* from agricultural ponds in southern Sweden, and focus on the quality of the terrestrial habitat surrounding the ponds and the metapopulation structure was suggested to help in explaining the observed phenomenon (Loman & Lardner 2006). My results indicate that increased isolation of breeding ponds caused by domination of agricultural lands and loss of wetlands, as well as habitat homogeneity are characteristics that could partly explain the absence of these amphibians in the studied agricultural habitats. Due to the importance of wetlands for amphibians, future agricultural intensification is likely to be an increasing threat to amphibian populations, because more lands will be drained and ponds filled, and also because agricultural wetlands have not been well protected in agri-environment schemes (Bradbury & Kirby 2006). Small constructed wetlands, which are used for the controlling of agricultural runoff, have been suggested as potential solutions for maintaining aquatic habitats in agricultural areas, and they have been estimated to be suitable habitats for many farmland species (Bradbury & Kirby 2006). However, I believe some reservations about their suitability are needed, as although these habitats may well be used by many farmland species, including amphibians, they may also be sources of particularly high pesticide concentrations. Hence, maintaining aquatic habitats with sufficient buffer strips is likely to be needed to ensure with high water quality.

In summary, due to the pervasiveness of modern-day agriculture and to the fact that amphibian breeding habitats are often situated in agricultural landscapes, agriculture undoubtedly is a factor influencing many amphibian populations. By conserving wetlands, controlling for the use of pesticides and by increasing habitat heterogeneity, we may have a better chance of maintaining viable amphibian populations and greater biodiversity in agricultural landscapes also in the future.

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