PLANT INVASIONS IN BOREAL AGRICULTURAL HABITATS – THE EFFECT OF ENVIRONMENTAL CONDITIONS, SPECIES TRAITS AND THE IMPACT ON NATIVE DIVERSITY

DOCTORAL THESIS
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ACADEMIC DISSERTATION
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## CONTENTS

List of original publications ................................................................. 4  
Contributions ...................................................................................... 4  
Abstract .............................................................................................. 5  

1 Introduction .............................................................................. 6  
  1.1 Terms and definitions .................................................. 6  
  1.2 Factors affecting the invasion level ......................... 8  
  1.3 The traits of succesful invaders.................................. 10  
  1.4 Propagule pressure and residence time ..................... 11  
  1.5 Impact of plant invasions ............................................. 11  
  1.6 Research needs .......................................................... 12  

2 Aims of the study ................................................................. 14  

3 Material and methods ........................................................... 15  
  3.1 Study area ................................................................... 15  
  3.2 Study design ................................................................ 16  
  3.3 Analyses of the data .................................................... 17  

4 Results and discussion .......................................................... 20  
  4.1 Spatial, temporal and habitat variation in invasion level (I, II) ................................................................. 20  
  4.2 The effects of environmental conditions on alien plants (I-IV) ............................................................. 21  
    4.2.1 Geographical location and climate constrain plant invasions (I-IV) ..................................................... 21  
    4.2.2 Complex effects of the disturbance regime (I-III). 23  
    4.2.3 Alien species favour species-rich sites (III)....... 23  
  4.3 Alien species traits are habitat-dependent and linked with environmental conditions (IV) ................................. 25  
  4.4 No evidence for negative impacts of alien species on native diversity (I, II, III) .................................................. 26  

5 Conclusions and implications for management and control. 28  
Acknowledgements .......................................................................... 32  
References .......................................................................................... 33
LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications:


The publications are referred to in the text by their roman numerals.

CONTRIBUTIONS

The following table presents the contributions of the authors to the original articles of this thesis:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
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MJ = Miia Jauni, TH = Terho Hyvönen, JH = Juha Helenius

*The sampling data are from MYTVAS project, from the national monitoring of species diversity in agricultural environment. The plant species section of MYTVAS is led by JH since 1995. For more, see Kuussaari et al. (2008).
ABSTRACT

Plant invasions cause a serious threat to native biodiversity. Agricultural habitats are highly disturbed and often invaded by the alien plant species. Generally, the success of a plant invader depends on the abiotic (e.g. climate, habitat properties) and biotic factors (e.g. the characteristics of the invader and interaction with the resident species). In this thesis, I (1) determined the invasion level and occurrence of alien plant species in Finnish agricultural habitats, (2) assessed the most important environmental factors affecting the invasion level, and the interaction between the environmental factors and the characteristics of the alien plant species, (3) studied the relationship between alien and native plant species diversity at multiple spatial scales, and (4) assessed the alien species impact on native species richness and diversity.

The invasion level of alien plant species varied between different types of semi-natural agricultural habitats, geographical regions and study years. Generally, more frequently disturbed and more intensively managed habitats (e.g. field and road verges) were more often invaded by alien plants than infrequently disturbed and managed habitats (e.g. grassland). However, the effect of disturbance regime tended to depend on residence time of the alien plant species, and vary among the alien plant species. The invasion level decreased towards north with dropping temperature and increased towards east with increasing continentality. The geographical trends may be explained by climate, migration history and land-use intensity. In addition, alien plant species diversity increased with increasing native plant species diversity. Thus, the results suggest that species interactions, especially competition, with resident plant species do not limit plant invasions in semi-natural agricultural habitats. The positive relationship between native and alien species may be caused by both suitable environmental conditions and spatial heterogeneity in environmental conditions partly created by disturbance of agricultural habitats. The species traits of alien plant species are habitat-specific and strongly related environmental conditions.

I did not find evidence that alien plants species cause a severe threat to native plant diversity in Finnish semi-natural habitats. The most harmful invasive plant species are still rare in Finnish agricultural landscape. In the future, the pressure of establishment and spread of alien species can be assumed to increase. Thus, regular monitoring is needed for early detection of new species and detection of the changes in the distribution and the spread of established alien species. The fact that plant invasions are species-specific and depended on environmental characteristics calls for habitat- and species-specific studies on the impacts of alien species and on the determinants of plant invasion at multiple spatial scales.
1 INTRODUCTION

Invasion ecology is a rapidly developing branch of ecology studying the human-mediated introductions of organisms, specifically introductions to areas outside their potential range as defined by their natural dispersal mechanisms and biogeographical barriers (e.g. Pyšek et al. 2004, Richardson and Pyšek 2006). Invasive alien species cause severe ecological, social and health hazards and economic losses, and are widely considered as one of the leading direct causes of biodiversity loss (e.g. Didham et al. 2005, Vilà et al. 2011).

In this thesis, alien plant species invasions on agricultural habitats are focused. Agriculture has intentionally and accidentally affected on the introduction and spread of alien plants (e.g. Weidema 2000) and created disturbed habitats, which are often invaded by alien plants (e.g. Chytrý et al., 2005, Pyšek et al. 2010a). In Finland, semi-natural agricultural habitats (e.g. semi-natural grasslands, wooded pastures) are important for species diversity and survival. For instance, almost third of the threatened vascular plants favour semi-natural agricultural habitats and ruderal habitats as their primary habitat (Rassi et al. 2010). Although, invasive alien plant species are known to threaten the native species diversity (e.g. Nummi et al. 2001, MMM 2012), the studies of alien plant invasion from the terrestrial habitats in Finland are scarce (but see Nummi et al. 2001, Valtonen et al. 2006, Hyvönen and Jalli 2011, Ranta and Viljanen 2011, Ramula and Pihlaja 2012).

Generally, the success of alien plant invasions depend on the characteristics of the invaded habitat (i.e. invasibility) and the species traits of the invading alien plant (i.e. invasiveness) (see Table 1 for terms). In the following sections, I will discuss about the abiotic and biotic factors affecting alien plant species, and the impacts of plant invasion.

1.1 TERMS AND DEFINITIONS

Although there have been several attempts to achieve unified framework for biological invasions and consolidate invasion terminology (Richardson et al. 2000, Colautti and Maclsaac 2004, Pyšek et al. 2004, Richardson and Pyšek 2006, Blackburn et al. 2011, Richardson et al. 2011), invasion ecology has a confusing range of concepts, terms and definitions, and the terminology is not standardized.

In this thesis, I considered an alien plant species as a species that have been introduced to a new region due to intentional or accidental introduction due to human activity (see Table 1). Invasive alien plant has been defined based on alien species impact on biodiversity or alien species ability to spread. I used the definitions of The Convention on
Biological Diversity (2002) and Finland’s National Strategy on Invasive Alien Species (MMM 2012), which defines invasive alien species as a species whose introduction and/or spread threatens biological diversity and/or cause economic, health and social hazards. Both of these definitions differ from the definition suggested by Richardson et al. (2000), who used reproduction and potential to spread over long distances as criterion for species classified as invasive, and excluded any connotation of impact, because well-established term of harmful species already exists i.e. weed and pest. The impact criterion is often used in policymaking and legislation, whereas the use of spread as a criterion is preferred by ecologists, because the impact criterion is more subjective, dependent on individuals’ values and the scale of the study, and the measurement of the impact is still controversial (e.g. Daehler 2001). The impact criterion is used by the North European and Baltic Network on Invasive Alien Species (NOBANIS 2012) and the Finland’s National Strategy on Invasive Alien Species (MMM 2012), from which I derived the information on the invasive alien plant species of Finland.

<table>
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<tr>
<th>Terms</th>
<th>Definition used in this thesis</th>
<th>Other definitions</th>
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<tr>
<td>Alien plant species (synonyms: exotic, introduced, non-indigenous, non-native)</td>
<td>Plant taxa in a given area whose presence there is due to intentional or accidental introduction as a result of human activity (Richardson et al. 2000).</td>
<td>A species, subspecies or lower taxon, introduced outside its natural past or present distribution; includes any part, gametes, seeds, or propagules of such species that might survive and subsequently reproduce (The Convention of Biological Diversity 2002).</td>
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<tr>
<td>Invasive plant alien</td>
<td>An alien species whose introduction and/or spread threaten biological diversity (The Convention of Biological Diversity 2002).</td>
<td>An alien plant that sustain self-replacing populations over several life cycles, produce reproductive offspring, often in very large numbers at considerable distance from the parent and/or site of introduction, and have the potential to spread over long distances (Richardson et al. 2011).</td>
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<tr>
<td>Weed</td>
<td>Plant (not necessarily alien) that grows in sites where they are not wanted and which usually have detectable economic or environmental effects (Richardson et al. 2000).</td>
<td>An alien plant introduced to Central Europe before 16th century, both deliberately or accidentally (e.g. Pyšek et al. 2004).</td>
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<td>Archaeophyte</td>
<td>An alien plant introduced to Finland before the early 17th century (Hämet-Ahti et al. 1998).</td>
<td>An alien plant introduced to Central Europe before 16th century, both deliberately or accidentally (e.g. Pyšek et al. 2004).</td>
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<tr>
<td>Neophyte</td>
<td>An alien plant introduced to Finland after the early 17th century (Hämet-Ahti et al. 1998).</td>
<td>An alien plant introduced to Central Europe after 16th century, both deliberately or accidentally (e.g. Pyšek et al. 2004).</td>
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Invasibility: The properties of a community, habitat or ecosystem that determine its inherent vulnerability to invasion (Lonsdale 1999, Richardson et al. 2011).

Invasion level: Actual number or proportion of alien species in a community, habitat or region, resulting from an interplay of its invasibility, propagule pressure and climate (Hierro et al. 2005, Chytrý et al. 2008a, Richardson et al. 2011).

Invasiveness: The features of alien organisms, such as their life-history trait and modes of reproduction that define their capacity to invade, i.e. to overcome various barriers to invasion (Richardson et al. 2011).

Residence time: The time since the introduction of a species to a region (e.g. Richardson et al. 2011).

Propagule pressure: A composite measure of the number of individuals released into a region to which they are not native. It incorporates estimates of the absolute number of individuals involved in any one release event (propagule size) and the number of discrete release events (propagule number) (Lockwood et al. 2005).

Invasion paradox: The interaction of scale and native–exotic richness patterns. Relates to contrasting lines of support for both negative and positive relationships between native biodiversity and various measures of ‘success’ of alien species (Fridley et al. 2007, Richardson et al. 2011).

Biotic resistance: Resistance by resident species to the establishment (or post-establishment survival, proliferation and spread) of alien species (Elton 1958, Richardson et al. 2011).

1.2 FACTORS AFFECTING THE INVASION LEVEL

Invasibility refers to the inherent vulnerability of the community, habitat or ecosystem to species invasions (e.g. Lonsdale 1999, Davis et al. 2005, Table 1). Invasibility should be separated from the invasion level, which integrates the effects of invasibility, propagule pressure and climate (e.g. Chytrý et al. 2008a, Pyšek et al. 2010). Habitats vary considerably in the invasion level, and these differences in the invasion level are mainly
caused by inherent habitat properties (e.g. Chytrý et al. 2008a, 2008b, Pyšek et al. 2010a). Generally habitats associated with human- and water-induced disturbances, high fertility, and high propagule pressure are highly invaded by alien plant species (e.g. Pyšek et al. 2010a). Agricultural habitats are among the most invaded habitats (e.g. Chytrý et al. 2005, Vilà et al. 2007). Agricultural habitats vary in their invasion level, and arable land is more often invaded by alien plants than semi-natural grasslands (e.g. Chytrý et al. 2005, Pyšek et al. 2009a).

Disturbance intensity and/or frequency have a strong role in the spread of alien plant species, and often heavily disturbed habitats, such as arable land and ruderal sites, are most invaded (e.g. Pyšek et al. 2010a). Disturbance may open new ground for colonization (e.g. Hobbs and Huenneke 1992), increase resource availability (e.g. Davis et al. 2000), limit species competition, and hence facilitate the susceptibility of a habitat to invasion (Belote et al. 2008, Simonová and Lososová 2008, Clark and Johnston 2010). However, different disturbances can have different effects on invasibility even in the same habitat, and species vary in their response to disturbance (Hobbs and Huenneke 1992, Smith and Knapp 1999). In addition, the effect of disturbance depends on the spatial scale: certain disturbances affect at local scale (e.g. clear cuts, grazing, soil disturbance) while others affect at landscape or regional scales (e.g. fragmentation, fire, hurricanes) (e.g. Hobbs and Huenneke 1992, Pauchard and Shea 2006).

Geographical location and climate (e.g. Grytnes et al. 1999, Lonsdale 1999, Sax 2001, Pyšek et al. 2002, Kivinen et al. 2006, Richardson and Pyšek 2006) have a major effect on the occurrence of plant species including aliens. High alien species richness has been reported to be associated with dry, warm climate and low altitude (e.g. Stohlgren et al. 2002, Gassó et al. 2009), while natives rather favour wet and cold climate (e.g. Pyšek et al. 2005). In boreal region of Europe, low level of invasion is predicted because of the humid, cool climate and low human population density (Chytrý et al. 2009). The environmental characteristics of the site must be suitable for invasion to occur (e.g. Richardson and Pyšek 2006, Catford et al. 2009). Often alien plant species favour mesic habitats with high availability of resources, such as light and nutrients (e.g. Rejmánek 1989, Alpert et al. 2000, Foster et al. 2002, Milbau and Nijs 2004). Several hypotheses attribute invasion to environmental characteristics and they are often based on fluctuation in resource availability (e.g. Davis et al. 2000, Catford et al. 2009). The invading species must have access to available resources, and they will be more successful at the invading a community if it does not encounter intense competition for the resources from resident species (Davis et al. 2000, Richardson and Pyšek 2006).

Species richness and the structure of the plant community may have a considerable effect on habitat invasibility (e.g. Dukes 2002, Stohlgren et al. 2002, Richardson and Pyšek 2006, Fridley et al. 2007). Elton’s (1958) theory of biotic resistance suggests a negative relationship between native species diversity and community invasibility due to species interactions,
such as competition. Most of the evidence on biotic resistance comes from small-scale experiments (e.g. Levine et al. 2000, Naem et al. 2000, Kennedy et al. 2002), while large-scale observational studies have mostly shown a positive relationship between diversity and invasibility (e.g. Stohlgren et al. 1999, Davies et al. 2005, Richardson and Pyšek 2006). This contradiction is termed as invasion paradox and it is mostly induced by spatial scale (e.g. Fridley et al. 2007). It is potentially explained by covarying external factors, such as geographical location, climate, and availability of resources (Shea and Chesson 2002). Spatial scale influences the invasion patterns, ecological processes and mechanisms (e.g. Pauchard and Shea 2006), and various factors contributing to invasibility are scale-dependent (e.g. Milbau et al. 2009). Thus the invasions of alien plant species are scale-dependent, and studies of plant invasions are affected by scale (e.g. Stohlgren et al. 2002, Pauchard and Shea 2006).

Human actions, such as international trade, travel, and transportation, are the most important predictor of biological invasion at the large spatial scale (e.g. Pyšek et al. 2010b, Essl et al. 2011). Economic and demographic variables, which reflect the intensity of human activities, have a strong impact on the invasion levels of alien plant species (e.g. Pyšek et al. 2010b). Human population size and various contemporary indicators of socioeconomic conditions are linked with regional numbers of alien plants (e.g. Hulme et al. 2009, Sharma et al. 2010, Essl et al. 2011). According to Sharma et al. (2010) the density of invasive alien species increases with human population density, total geographic area, human development index and the gross domestic product.

### 1.3 THE TRAITS OF SUCCESSFUL INVADERS

Many studies have attempted to profile successful invader, and have identified species traits related to reproduction, growth, dispersal, competitive ability, habitat preferences and invasion history as important correlates of invasiveness (e.g. Thompson et al. 1995, Rejmánek 1996, Prinzing et al. 2002, Lloret et al. 2005, Pyšek and Richardson 2007, Pyšek et al. 2009b). However, it has appeared to be difficult to identify species traits associated with invasiveness that would consistently apply to all alien plant species across different environmental conditions worldwide (e.g. Alpert et al. 2000, Lloret et al. 2005, Richardson and Pyšek 2006). One of the principal reasons is that species traits of a successful invader depend on the characteristics of the habitat (Pyšek et al. 1995, Thompson et al. 1995, Alpert et al. 2000).

In agricultural habitats, such as grasslands and arable fields, annuals and therophytes are a common group of plants among native and alien weed species (e.g. Sutherland 2004, Lososová et al. 2008). The most important traits for abundant weed species in temperate region are those
that enable weeds to grow and reproduce in the cool season (e.g. requirements for low temperature, annual, CR strategist), and those that are adaptations to growth in dense vegetation and in highly productive habitats (e.g. high nutrient uptake, shade tolerance) (Lososová et al. 2008). However, in disturbed habitats, such as agricultural habitats, different species traits contribute to the success of alien species under different disturbance types (Pyšek et al. 1995, Lake and Leishman 2004). Although species traits of a successful invader are known to vary according to the habitat type and environmental conditions, the interaction has largely been ignored in the empirical studies in quest of species traits in successful plant invasions (but see Thompson et al. 2001, Lake and Leishman 2004, Lososová et al. 2006, Thuiller et al. 2006, Pyšek et al. 2009b).

1.4 PROPAGULE PRESSURE AND RESIDENCE TIME

In addition to invasibility of the habitats and species traits (i.e. invasiveness), factors such as propagule pressure and residence time should be considered when predicting and understanding plant invasions (e.g. Milbau et al. 2009). Propagule pressure affects both the invasibility of the habitat and the ability of the species to spread into new areas (e.g. Colautti et al. 2006, Simberloff 2009) and it is a key element to understanding the success and failure of alien plant invasions (Lockwood et al. 2005).

Residence time represent another dimension of propagule pressure. It is an important determinant of present geographical range sizes of alien plants (Pyšek and Jarošík 2005, Rejmánek et al. 2005, Williamson et al. 2009). The longer species is present in the area the more propagules are spread, and the higher their chance is to establish and invade over larger range (Pyšek and Jarošík 2005). Generally, it takes at least 150 years for an alien plant species to reach their maximum (Williamson et al. 2009), thus many neophytes (see Table 1 for definitions) have probably not yet occupied all suitable habitats. In addition, residence time is associated with the alien species response to environmental conditions. For instance, in Central Europe neophytes prefer wet, fertile habitats, while archaeophytes are more common in sunny, dry to mesic habitats (Chytrý et al. 2005, Pyšek et al. 2005, Simonová and Lososová 2008).

1.5 IMPACTS OF PLANT INVASIONS

Invasive alien species cause severe ecological hazards, and are widely considered as one of the leading direct causes of biodiversity loss (e.g. Didham et al. 2005, Vilà et al. 2011) (see however Davis et al. 2011).
Invasive alien species may impact on native species by competing for resources, facilitating the spread of pathogens, and through hybridisation and impacts on higher trophic levels (e.g. Levine et al. 2003, Hulme 2007). In addition, invasive alien plants can transform the structure and function of the ecosystems by, for example, changing nutrient cycling and disturbance regime (e.g. Mack and D’Antonio 1998, Levine et al. 2003, Rejmánek et al. 2005). However, the impact of invasive plants on biodiversity is less severe than impact of alien pathogens, herbivores and predators, and not a single native plant species has been documented to being driven to extinction by competition from alien plants alone (e.g. Rejmánek et al. 2005). The ecological impacts of invasive alien plant species are largely species-specific and the severity of the impacts depends on the identity of the invading species (Hejda et al. 2009, Vilà et al. 2011).

In addition to ecological impacts, invasive alien plants cause economic, social and health detriments. Many alien plants have become weeds, which cause crop losses and control costs (e.g. Pimentel et al. 2000, Vilà et al. 2010). In addition, alien plant species can reduce availability of pollinators to native species, and decrease the recreational and aesthetic values of the landscape (e.g. Pyšek et al. 2009b, Vilà et al. 2010). For instance, *Rosa rugosa* Thunb. ex Murray grows in abundant, thorny thickets in the Nordic beaches, reducing recreational use of the beaches (e.g. Weidema 2000, Vilà et al. 2010, MMM 2012). Several alien plants can also cause allergies or other severe health problems (e.g. Vilà et al. 2010), such as burn and blisters induced by *Heracleum mantegazzianum* Sommier & Levier (e.g. Weidema 2000). Many invaders are known to cause multiple impacts, but the current understanding is often restricted to relatively few dominant species (e.g. Pyšek et al. 2009a, Vilà et al. 2010, 2011). Although invasive alien plant species have severe impacts, the impacts are heterogeneous and vary even within particular impact type (e.g. Vilà et al. 2011).

### 1.6 RESEARCH NEEDS

Although agricultural habitats are among the most invaded habitats (e.g. Lonsdale 1999, Chytrý et al. 2005, Pyšek et al. 2010a), the studies of the temporal, spatial and within-habitat variation in the invasion level of alien plants in agricultural habitats are lacking. In addition the factors contributing to the invasion level have been studied insufficiently (but see Thompson et al. 2001, Lake and Leishman 2004, Leishman and Thompson 2005, Thuiller et al. 2006), especially in the boreal region. Species vary in their response to environmental conditions (e.g. Richardson and Pyšek 2006) and in their effect on native species diversity (e.g. Stohlgren et al. 1999, Vilà et al. 2011). However, species-specific studies on the effect of environmental conditions and impact on native species diversity are inadequate, especially on less dominant alien plant
species (e.g. Pyšek et al. 2009a, Vilà et al. 2010, 2011). In addition, the studies of alien plant invasion on the terrestrial habitats in Finland are scarce (but see Nummi et al. 2001, Valtonen et al. 2006, Hyvönen and Jalli 2011, Ranta and Viljanen 2011, Ramula and Pihlaja 2012), and the studies on the effects on environmental conditions on alien plant species are lacking.

One of the factors affecting plant invasions is the native species diversity, and several processes have been identified to generate either positive or negative native-alien richness relationships (e.g. Fridley et al. 2007). These processes are related to spatial scale, which emphasize the importance to study native-alien relationships at multiple spatial scales. However, only few studies have estimated the effect of different processes at multiple spatial scales taking into account also species diversity components operating at multiple scales (e.g. Davies et al. 2005, Stohlgren et al. 2006, Capers et al. 2007, Belote et al. 2008, Veech and Crist 2010). In addition to features of the habitat and ecosystem, the success of plant invasions depends on the characteristics of the invading plant species. Although characteristics of a successful plant invader are known to be habitat-specific and affected by environmental features, empirical studies of the characteristics of successful invader have largely ignored the environmental conditions (but see Thompson et al. 2001, Lake and Leishman 2004, Leishman and Thompson 2005, Thuiller et al. 2006).
2 AIMS OF THE STUDY

In this thesis, I will assess the temporal, spatial and within-habitat variation in the invasion level in Finnish agricultural habitats, and examine how environmental conditions and species characteristics contribute to the level of invasion and to the occurrence of alien plant species. In addition, I assess the effect of plant invasion on native plant diversity. I aimed at answering to the following questions:

1. Which are the invasion levels of alien plant species in five different agricultural habitats (I) and four different geographical (II) regions in Finland?
2. How environmental factors affect on the invasion level and the occurrence of alien plant species (I), and what is the impact of alien plant species on the native plant species richness and diversity (II)?
3. What is the relationship between native and alien plant species diversity in agricultural habitats at multiple spatial scales, and which processes contribute to these diversity-invasibility relationships? (III)
4. Which are the characteristics of a successful plant invader and how these characteristics are related to habitat characteristics? (IV)
3 MATERIALS AND METHODS

3.1 STUDY AREA

In this study, I used a comprehensive data from long-term national monitoring study on the effects of the Finnish agri-environment support scheme (MYTVAS) (Kuussaari et al. 2008). The data were collected from agricultural landscapes situated in four geographical regions in Finland: south, south-western, western and eastern Finland (Fig. 1). The southern and south-western regions are situated in hemiboreal and southern boreal zones, and western and eastern regions in the middle boreal zone (Ahti et al. 1968). Southern and south-western regions have the most advantageous climatic and edaphic conditions for crop production in Finland (percentage of cultivated field 50.9% and 58.6%, respectively), whereas western and eastern Finland are characterized by cooler climate, a shorter growing season and lower proportion of arable land (42.4% and 27.4%, respectively) than in southern and south-western Finland (e.g. Kivinen et al. 2006, Kuussaari et al. 2008, Tarmi et al. 2009). In the western Finland, the typical agricultural landscape is dominated by intensively cultivated arable land, surrounded by coniferous forests and mires, whereas eastern Finland is characterized by extensive forest cover (59.3%), and agriculture is based mainly on dairy farming (e.g. Kivinen et al. 2006, Kuussaari et al. 2008, Tarmi et al. 2009).

In Finland, approximately 1 300 vascular plant species are regarded as established, and roughly 550 terrestrial vascular plants are alien to Finland (e.g. Weidema 2000, MMM 2012). Hyvönen and Jalli (2011) assessed the number of agricultural weed species in Finland, and detected 815 alien weed species, most of which (501, 61%) were casual neophytes. Thus, most of the alien weeds are found in Finland occasionally, and the circumstances for establishment of permanent population have not been favourable (e.g. climate conditions; Hyvönen 2011, Hyvönen et al. 2011), although the propagule pressure is high (Hyvönen and Jalli 2011). In the future, established neophytes are expected to extend their distribution and increase their occupation in agricultural habitats, and climate change may affect the establishment of the casual neophytes (Hyvönen and Jalli 2011). According to the Finland’s National Strategy on Invasive Alien Species (MMM 2012), 24 alien plant species (~4% of all alien plant species) are regarded as invasive in Finland. Invasive alien plant species are known to have negative effect on native species diversity, species composition and ecosystems structure (e.g. Valtonen et al. 2006, MMM 2012). Semi-natural agricultural habitats (e.g. semi-natural grasslands, wooded pastures) and ruderal habitats are a primary habitat for almost third of the threatened vascular plants in Finland (Rassi et al. 2010).
The MYTVAS vascular plant data (Kuussaari et al. 2008) comprised a total of 52 sites (1 km²), and each site was divided into four squares (Fig. 1). Among these squares (0.25 km²) two most divergent squares were selected in order to represent the landscape heterogeneity within the 1 km² site (Kuussaari et al. 2004). Vascular plants were recorded from six 50 m × 1 m transects lines in each 0.25 km² square, and from three quadrats (1 m²) along each transect. Thus, the hierarchical data set comprised five spatial scales: 1 m² quadrats, 50 m² transects, 0.25 km² squares, 1 km² sites and regions.

The transects were situated in five distinct habitat type: (1) field margin (margin between two agricultural fields), (2) forest margin (margin between a forest and an agricultural field), (3) road margin (margin between a road and an agricultural field or road verge within agricultural habitat), (4) grassland (including uncultivated meadows, abandoned fields and cultivated or natural pastures) and (5) other habitat types (including margin between agricultural field and a waterway, cart-tracks and other habitats low in number). In addition to habitat type, environmental variables included several variables measured at different spatial scales. At 1 m² quadrats, data included local environmental variables (total vegetation coverage, proportion of bare ground and rockiness). Environmental variables measured at 50 m² transects included spatial variables (longitude...
3.2 STUDY DESIGN

The MYTVAS vascular plant data (Kuussaari et al. 2008) comprised a total of 52 sites (1 km²), and each site was divided into four squares (Fig. 1). Among these squares (0.25 km²) two most divergent squares were selected in order to represent the landscape heterogeneity within the 1 km² site (Kuussaari et al. 2004). Vascular plants were recorded from six 50 m × 1 m transects lines in each 0.25 km² square, and from three quadrats (1 m²) along each transect. Thus, the hierarchical data set comprised five spatial scales: 1 m² quadrats, 50 m² transects, 0.25 km² squares, 1 km² sites and regions.

The transects were situated in five distinct habitat type: (1) field margin (margin between two agricultural fields), (2) forest margin (margin between a forest and an agricultural field), (3) road margin (margin between a road and an agricultural field or road verge within agricultural habitat), (4) grassland (including uncultivated meadows, abandoned fields and cultivated or natural pastures) and (5) other habitat types (including margin between agricultural field and a waterway, cart-tracks and other habitats low in number). In addition to habitat type, environmental variables included several variables measured at different spatial scales. At 1 m² quadrats, data included local environmental variables (total vegetation coverage, proportion of bare ground and rockiness). Environmental variables measured at 50 m² transects included spatial variables (longitude
and latitude), habitat quality (shadiness, moisture, average vegetation height) and disturbance regime (proportion of bare ground, mowing). Variables of geographical location and landscape diversity were measured at 0.25 km$^2$ squares, and climatic variables (including total summer temperature sum and precipitation, total number of frost days and starting date of the growing season) were calculated at 1 km$^2$ sites. In addition, I collected species trait data of 17 species characteristics, which represented the ecological and morphological traits, and traits related to invasion history, dispersal and species requirements for environmental conditions, from several databases, such as BiolFlor (Klotz et al. 2002) and LEDA traitbase (Kleyer et al. 2008).

3.3 ANALYSES OF THE DATA

Invasibility can be characterized by the survival rate of invading species, but it is difficult to quantify, because the influence of species invasiveness and propagule pressure on invasion level must be accounted for (e.g. Chytrý et al. 2008a, Pyšek et al. 2010a, Catford et al. 2012). As a precondition for quantifying invasibility is possibility to compare invasion level across habitats and ecosystems (e.g. Catford et al. 2012). Invasion level of alien species can be used to assess the extent or severity of invasions, and to reveal spatio-temporal trends (Chytrý et al. 2008a, Catford et al. 2012). In addition, invasion level can act as an early warning sign for ecological degradation and as an estimate for the consequences of invasion (Catford et al. 2012). I assessed the invasion level for five different habitat types (I) and four different geographical regions (II) using relative alien species richness (I and II) and alien species diversity (measured as Shannon-Wiener diversity index) (II). The invasion level can change in time depending on the identity of alien species present, propagule pressure and biotic and abiotic conditions (e.g. Catford et al. 2012). I assessed changes in the levels of invasions over a decade (II). In addition, I calculated the frequencies of occurrence of neophytes for each study year.

The invasion level is affected by several environmental factors, such as climate, geographical location, the structure of the plant community and habitat properties (e.g. Chytrý et al. 2008a, Pyšek et al. 2010a). I examined how these environmental factors affect on species richness and occurrence (I, II). Native species, archaeophytes and neophytes were examined separately (I), because their response to environmental conditions varies (e.g. Chytrý et al. 2005, Pyšek et al. 2005, Simonová and Lososová 2008, Pyšek et al. 2010a). Because species vary in their response to disturbance and other environmental variables (e.g. Hobbs and Huenneke 1992, Smith and Knapp 1999), I also determined the effect of environmental conditions on the most common neophyte species (*Achillea ptarmica* L., *Epilobium adenocaulon* Hausskn., *Galium album* Mill.)
and *Trifolium hybridum* L.) (II). These analyses were conducted with a combination of principal components (PCA) and generalized linear mixed models (GLMM) analyses. PCA summarizes the environmental data, and reduce the multicollinearity among the environmental variables (e.g. Kent and Coker 1992), whereas GLMM allows the use of non-normal distributions and the incorporation of random terms that control for spatial non-independence (e.g. Bolker et al. 2009).

I examined the relationship between native and alien species richness using generalized linear models (III). In order to understand the drivers of these relationships we included alpha, beta and gamma diversity in the analyses. The relationship between native and alien species is strongly associated with spatial scale, and driven by species interactions (e.g. competition) and environmental conditions (e.g. Shea and Chesson 2002, Pauchard and Shea 2006, Stohlgren et al. 2006, Pyšek et al. 2010a). Thus, I analysed how the environmental variables describing geographical location, productivity, disturbance regime and landscape structure affected diversity components of alien and native plant species at three spatial scales (1 m² quadrats, 50 m² transects and 0.25 km² squares).

In addition to environmental conditions, the success of an alien plant species depends on the species traits of the invading plant species. In the search for the characteristics of successful invader, I studied the differences between neophytes and native species using Fisher’s exact test with sequential Bonferroni correction (IV), which is more accurate than asymptotic tests of independence for small, sparse data and small expected values (e.g. Mehta and Patel 1999). The sequential Bonferroni correction avoids the probability of type I errors, which may be inflated when performing multiple tests (e.g. Holm 1979). Since species traits are habitat-dependent (e.g. Thompson et al. 1995, Lloret et al. 2005), I assessed the interaction between environmental factors (habitat preferences, climate, geographical location) and characteristics of neophytes by using RLQ analysis combined with Hartigan’s K means clustering method (see e.g. Thuiller et al. 2006). RLQ analysis is a multivariate method (IV), which enables study of relationship between species traits and environmental conditions, and can reveal processes that remain hidden when analyzing environmental factors and species characteristics separately (e.g. Dolédec et al. 1996). The Hartigan’s K means clustering was used to define functional groups of neophytes sharing similar traits and similar responses to environmental conditions. In addition, with Moran’s I randomization test (e.g. Cliff and Ord 1973) I tested whether the clusters were phylogenetically independent.

I used the invasion levels, occurrence of the neophytes and comparisons between invaded and uninvaded sites in order to estimate the effect of neophyte invasion to native species diversity (I, II). I tested the differences in native species richness and native diversity (measured as Shannon-Wiener diversity index) between invaded and uninvaded by the
most common neophytes in 50 m$^2$ transects using a t-test or a Kruskal-Wallis test if the equality of the variances was not attained (II).
4 RESULTS AND DISCUSSION

4.1 SPATIAL, TEMPORAL AND HABITAT VARIATION IN INVASION LEVEL (I, II)

I found that invasion level of alien plants varied between different semi-natural agricultural habitats (I), geographical regions, and the study years (II). The results were sensitive to the method of measuring the invasion level (either by relative alien species richness or alien species diversity).

Relative alien species richness was highest in frequently disturbed and more intensively managed habitats, such as field margins and road margins in agricultural landscape, whereas infrequently disturbed and managed grasslands were more seldom invaded by the alien plants. This result is consistent with previous studies (e.g. Chytrý et al. 2005, 2008b, Pyšek et al. 2010a) indicating that agricultural and ruderal habitats with human-induced disturbances, high fertility and propagule pressure exhibit highest levels of invasion.

The invasion level was strongly dependent on geographical location (I, II). For instance, relative alien species richness was higher in southern and south-western Finland than in eastern and western Finland. Thus, invasion level decreased northward with decreasing temperature and increased towards east with increasing continentality. This may be partially explained by the more favourable climate, migration history and routes, and land-use history and intensity (e.g. Luoto 2000, Kivinen et al. 2006). For instance, plant diversity of field margins is lowest in the most intensive cereal production areas of the south-western and southern Finland and highest in areas of mixed farming in the eastern Finland (Tarmi et al. 2002, 2009). Similar geographical trends related to latitude have been detected globally, and alien species richness often decreases towards poles (e.g. Lonsdale 1999). Consistent with previous studies, I found that the invasion level tended to be lower in northern boreal semi-natural habitats than in agricultural habitats of central and southern Europe (e.g. Vilà et al. 2007, Chytrý et al. 2009) (I). However, in the most disturbed Finnish semi-natural agricultural habitats, invasion level of alien plants may reach the same level as in ruderal habitats in central and southern Europe (e.g. Chytrý et al. 2008b).

In addition to spatial and habitat variation, the invasion level varied between to study years (II). For instance, alien species diversity was lower in 2005 than in other study years. The temporal variation in alien species diversity may be explained by variation in climatic conditions (e.g. precipitation was higher in 2005 than average, see Kuussaari et al. 2008), disturbance regime and fluctuation in resource availability (e.g. nutrients, water and light) (e.g. Davis et al. 2000, Richardson and Pyšek 2006). To overcome problems related to largely stochastic variation in environmental
conditions, a longer monitoring period would have been needed to detect the temporal changes in the invasion level. In addition, temporal variation was depended on the measure used for invasion level. I discovered no clear temporal variation in relative alien species richness, but in alien species diversity (as Shannon-Wiener diversity index) lower values were detected in 2005 than in the other study years. High alien species richness may indicate that the alien species are present in high numbers but contribute evenly to alien species abundance (e.g. Catford et al. 2012). Thus, stochastic variation in environmental conditions may not increase the alien species richness, but may affect the abundance of more dominant alien species. Although diversity provides information of the relative dominance of the species, the use of alien species diversity as a measure of invasion level may be problematic, because the interpretation of the findings can be difficult due to complex calculations of diversity indices (Catford et al. 2012). On the other hand, relative alien species richness, which indicates the contribution of alien species to a community, is easy to measure and interpret, independent of scale, and comparable across regions and ecosystems (Catford et al. 2012).

4.2 THE EFFECT OF ENVIRONMENTAL CONDITIONS ON ALIEN PLANTS (I-IV)

I found that the occurrence of alien plant species and the invasion level are strongly affected by environmental features, such as geographical location, climate, habitat type, disturbance regime and native species diversity. However, the relationship between environmental conditions and alien plant species depends on residence time, spatial scale and the species in question. In the following sections, I discuss, how these features are particularly related to three different environmental variables: (1) geographical location and climate, (2) disturbance regime, and (3) native species diversity.

4.2.1 Geographical location and climate constrains plant invasions (I-IV)

Generally, climate and geographical location have been considered as dominant environmental factors at larger spatial scales, such as continental (2 000-10 000 km²), regional (200-2 000 km²) and landscape scale (10-200 km²) (Milbau et al. 2009). My results support this assumption, indicating that at 0.25 km² scale, alien species richness was more strongly related to geographical location and climate than to landscape composition and local environmental conditions (III). In addition, my results highlight the importance of climate and geographical location also at smaller spatial scales (50 m²) (I, II, IV). Consistent with previous
studies (e.g. Grytnes et al. 1999, Kivinen et al. 2006), my results indicated that climate is strongly related to geographical location (I), thus these variables must be considered simultaneously. Generally, species richness of alien and native plant species increased towards north with decreasing temperature. As previous studies have shown (e.g. Simonová and Lososová 2008, Gassò et al. 2009), this decreasing trend tend to be stronger to alien species (including archaeophytes and neophytes) than to native species. In addition, invasion level increased towards east with increasing continentality due to migration history and routes, and land-use history and intensity (e.g. Luoto 2000, Tarmi et al. 2002, Kivinen et al. 2006, Tarmi et al. 2009).

Generally, neophytes and archaeophytes tended to respond similarly to climate and geographical location (I). However, residence time tended to be associated with geographical location even within neophytes (IV). The species that had arrived earlier (17th century) were associated with more eastern and northern location than the latecomers (20th century). For instance, Achillea ptarmica was more strongly related to longitude than other common neophyte species (II). Thus, the longer an alien species have been introduced, the better it has adapted to the climatic conditions, the more abundant it is, and the greater the seed bank and the probability of dispersal are (e.g. Hamilton et al. 2005, Pyšek and Jarošík 2005, Richardson and Pyšek 2006). However, many of the invasive alien plants, such as highly invasive Sambucus racemosa L. and Epilobium adenocaulon, do not occur in northern Finland, although they have arrived in Finland over 100 years ago (see Lampinen and Lahti 2011). The current distributions may be limited by harshening climatic conditions towards north of Finland (e.g. Hyvönen and Jalli 2011, Hyvönen et al. 2011).

In the future, climate may broaden the distribution areas of alien plant species (e.g. Walther et al. 2009), and be a driver of latitudinal shift of alien plant species (Guo et al. 2012). Changes in the climatic conditions may affect the likelihood of alien plant species to invade in to new areas and to naturalize (Walther et al. 2009). In Finland, climate change may increase the establishment of new alien species in the northern regions (Hyvönen et al. 2011). However, the relationship between plant invasions and climate change is complex (e.g. Bradley et al. 2010), and the responses of alien species to climate change are highly species-specific (e.g. Guo et al. 2012). In Finland, the climate change may increase the annual temperature, prolong the growing season (Jylhä et al. 2004), and thus enables successful reproduction, survival and establishment of alien species in the introduced region (Walther et al. 2009). Unlike temperature, the latitudinal gradient of seasonal changes in day length does not vary with climate change (Saikkonen et al. 2012). Thus, the successful poleward shift of alien plant species requires adaptation to the seasonality in day length and light quality (Saikkonen et al. 2012). In addition, the distribution of some alien plant species may be limited by their preferences
for calcareous soils, which are limited in areas in Finland (Hyvönen and Jalli 2011).

### 4.2.2 Complex effects of the disturbance regime (I-III)

Consistent with previous studies (e.g. Chytrý et al. 2005, Pyšek et al. 2010, Moles et al. 2012), alien species tended to be most dominant in disturbed, highly modified and intensively managed sites (I). Disturbance may facilitate plant invasions by creating new ground for colonization, increasing resource availability and/or propagule pressure, limiting competition from the resident species, and maintaining an open vegetation canopy (e.g. Smith and Knapp 1999, Davis et al. 2000, Celesti-Grapow et al. 2006, Belote et al. 2008). However, different types of disturbance can have different effect on alien species richness even in the same habitat (Smith and Knapp 1999). I discovered that the species number of archaeophytes and neophytes increased with increasing proportion of bare ground, but mowing tended to increase only the species richness of archaeophytes (I). Thus, the effect of the disturbance regime may also vary according to the resident time of the alien plant species.

In addition, the effect of different types of disturbance can vary among alien plant species. For instance, *Achillea ptarmica* and *Galium album* were more strongly associated with mowing, whereas *Epilobium adenocaulon* and *Trifolium hybridum* were more strongly related to the proportion of bare ground (II). Thus, alien species should not be viewed as a single group of species with similar responses to the same level of disturbance (Hobbs and Huenneke 1992). In addition and consistent with previous studies (e.g. Milbau et al. 2009), disturbance acts mainly at small spatial scales. The effect of disturbance was evident especially at rather small spatial scale (50 m² scale) (III). Previous studies indicate that the change in disturbance regime is a better predictor of plant invasions than disturbance itself (Moles et al. 2012), whereas my results suggest that both average disturbance and variation in disturbance affect on alien species diversity.

### 4.2.3 Alien species favour species-rich sites (III)

The classic theory of biotic resistance predicts that communities with high native species richness are more resistant to invasions than relatively simple plant communities (Elton 1958). A negative relationship between native and alien species is expected in sites where species interactions, especially competition, limit invasibility and environmental conditions are relatively constant (e.g. Elton 1958, Shea and Chesson 2002, Davies et al. 2005). Biotic resistance is generally applicable to small-scale experiments (e.g. Levine 2000, Naeem et al. 2000, Kennedy et al. 2002), whereas
observational studies at larger spatial scales indicate a positive correlation between native and alien species richness (e.g. Stohlgren et al. 1999, 2003, Davies et al. 2005, Gilbert and Lechowicz 2005). Because of this scale-dependence in the diversity-invasibility relationships, I examined the relationships at multiple spatial scales: 1 m², 50 m² and 0.25 km² using three diversity components: α-, β- and γ-diversity. Against expectations, I did not observe a negative correlation between native and alien species richness, but my results showed a positive alien-native relationship across spatial scales. Thus, competition did not limit invasibility at semi-natural agricultural habitats even at smallest spatial scale.

In order to understand the processes underlying the positive native-alien relationship, I tested two hypotheses: (1) biotic acceptance (e.g. Stohlgren et al. 2003, Gilbert and Lechowicz 2005, Stohlgren et al. 2006), and (2) spatial heterogeneity hypothesis (Davies et al. 2005). According to biotic acceptance hypothesis, environmental conditions that promote native species diversity also favour alien species diversity, when diversity is not limited by competition (e.g. Stohlgren et al. 2006). My results suggested that alien and native diversity responded similarly to some environmental variables (e.g. geographical location at 0.25 km²), but differently to some (e.g. landscape diversity at 0.25 km²) indicating that also other processes than biotic acceptance contribute to the positive native-alien relationship.

The spatial heterogeneity hypothesis assumes that landscapes with greater spatial heterogeneity in environmental conditions have suitable niches for both alien and native species, leading to positive native-alien relationship (Davies et al. 2005). Usually, this hypothesis has been applied to broader spatial scale because environmental conditions are expected to be rather homogeneous at small spatial scales. However, agricultural habitats generally have high spatial heterogeneity (e.g. Simonová and Lososová 2008) which may be perceived even at small spatial scales. My results showed that alien and native diversity were affected by both average and variability in local conditions, thus biotic acceptance and spatial heterogeneity hypothesis may not be mutually exclusive (e.g. Belote et al. 2008). In addition, I studied relatively disturbed, agricultural habitats, which are often invaded by alien plants (e.g. Chytrý et al. 2005, Pyšek et al. 2010). By creating more spatial heterogeneity and suitable niches, increasing resources availability and limiting species competition (e.g. Celesti-Grapow et al. 2006, Belote et al. 2008, Clark and Johnston 2011), disturbance may contribute to the positive native-alien relationship in agricultural habitats even at small spatial scales.
4.3 ALIEN SPECIES TRAITS ARE HABITAT-DEPENDENT AND LINKED WITH ENVIRONMENTAL CONDITIONS (IV)

I found that the trait composition of native species and neophytes were similar for most of the studied species traits, and differed only for four attributes: life form and preferences for temperature, moisture and soil fertility. In agreement with previous studies (e.g. Pyšek et al. 1995, Prinzing et al. 2002), my results indicated that alien species are more often therophytes and phanerophytes with preferences to warm, dry or mesic, nutrient-rich sites, whereas native species favour more often cold, moist and nutrient-poor sites. However, these patterns varied according to the habitat type. In more frequently disturbed field and road margins, the species traits of neophytes differed more from the traits of native species than in less frequently disturbed forest margins and grasslands. In addition, alien and native species tended to be even more similar within specific habitat type giving more support to the understanding that native and alien species share the same traits (Thompson et al. 1995, Lososová et al. 2008, Ordonez et al. 2010) than to the understanding that traits of native and alien species diverge (e.g. Pyšek et al. 1995, Sutherland et al. 2004, Pyšek and Richardson 2007).

In addition to habitat type, the traits of alien plant species were related to environmental condition, i.e. biogeographical location, temperature, disturbance, and quality of the site measured as moisture and light availability of the site. For instance, in moist, open, disturbed field margins successful alien plants were related to small, wind-dispersed seeds and nutrient-rich sites, whereas in dry to mesic, shady sites alien plant species were more often phanerophytes with seed dispersed by animals or mechanically. Previously, small, wind-dispersed seeds as an adaptation to enhanced colonization ability and long-distance dispersal have been associated with disturbed, fertile habitats (e.g. Lake and Leishman 2004). In addition, species traits varied according to climate conditions and geographical location due to invasion history, management intensity and the residence time of the alien species. The phylogenetic relatedness did not explain similarities in species traits nor the success of alien species (see e.g. Cadotte et al. 2009). Alien species with similar species traits occurred in different habitats affected by different environmental conditions regardless of their phylogenetic origin. My results demonstrate that species traits are habitat-dependent, and also strongly associated with environmental conditions (see e.g. Pyšek et al. 1995, Thompson et al. 1995, Alpert et al. 2000). In addition, my results support the understanding that it is impossible to found attributes for a successful invader that would be applied globally across different environmental conditions (e.g. Alpert et al. 2000, Richardson and Pyšek 2006).
4.4 NO EVIDENCE FOR NEGATIVE IMPACTS OF ALIEN SPECIES ON NATIVE DIVERSITY (I, II, III)

Alien plant species have twofold consequences for the biodiversity of agricultural landscapes: (1) they support biodiversity by contributing to the regional species pool, and/or (2) they threaten the biodiversity. I found evidence mainly on the former. Approximately, third of the plant species occurring in Finnish agricultural habitats were alien species, and most of the alien species (roughly 80%) were archaeophytes, which had established their populations a long time ago (I). Thus, alien plant species, especially archaeophytes, contribute considerably to the species pool of Finnish agricultural habitats.

I found that several alien species that are considered highly invasive in Finland, such as *Heracleum mantegazzianum* Sommier & Levier, *Impatiens glandulifera* Royle and *Avena fatua* L (MMM 2012), were not detected from semi-natural agricultural habitats of Finland (II). Thus, my results indicate that invasive neophytes are not widely established in these agricultural habitats, although they may be established in other habitats. Invasive neophytes, such as *Lupinus polyphyllus* Lindl., *Calystegia sepium* (L.) R.Br. and *Symphytum officinale* L., were mainly rare in agricultural habitats (I, II), although most of them favour agricultural and ruderal habitats (e.g. Hämet-Ahti et al. 1998). The establishment and spread of invasive neophytes may be hindered by the harsh climate in Finland and high proportion of forests in Finnish agricultural landscapes (e.g. Luoto 2000). In addition, most of the invasive neophytes have arrived to Finland over 100 years ago and are already established in Finland (e.g. Hämet-Ahti et al. 1998, Hyvönen and Jalli 2011). Generally, the longer the alien species are present in the area the higher their chance to establish and spread to new areas (Pyšek and Jarošík 2005). Usually, it takes at least 150 years for naturalized alien species to reach their maximum distribution range (e.g. Williamson et al. 2009). For that reason, most of established neophytes can still be expected to expand their ranges in Finland, even without major mitigation in the limiting factors, and increase their occupation of agricultural habitats (Hyvönen and Jalli 2011). In addition, the pressure of naturalization of alien plant species will continue in Finland, and the naturalization and invasion of alien plant species will be increasingly enhanced by the climate change (Hyvönen and Jalli 2011). In addition, the global change with increasing resource availability, global commerce and changes in land use or land cover may facilitate plant invasions (Bradley et al. 2010). Thus, regular monitoring is needed for the early detection of new alien species, detection of changes in the distribution and spread of the naturalized species, and in order to direct the control and management methods efficiently.

Interactions between invading and resident species, such as intensive competition may also hamper the establishment and spread of
invasive neophytes (Levine et al. 2003, Richardson and Pyšek 2006). However, I found no evidence that species interactions could limit the diversity on alien and native plant species in agricultural habitats even at fine spatial scales (III). This may result from niche processes, such as favourable and heterogeneous environmental conditions, including disturbance regime, resource availability and propagule pressure (e.g. Davies et al. 2005, Fridley et al. 2007, Belote et al. 2008). In addition, species-specific study of the impacts of most common alien species on native diversity indicated that alien species were positively associated with the native species richness and diversity (II). Even common invasive alien plants, *Galium album* and *Epilobium adenocaulon*, did not decrease the diversity of native plant species. However, my studies revealed only the impacts on native plant species richness and diversity, but not the ecological impacts on single native species, other trophic levels or the functioning of the ecosystem. Thus, further studies on the multiple impacts of invasive alien species is needed, and the studies should not be limited only to the most dominant species (e.g. Pyšek et al. 2009a, Vilà et al. 2010, 2011). In addition, I found that *Achillea ptarmica* was more strongly and positively affected by native diversity than other studied common neophytes (II). This result suggests that alien species’ impacts on native diversity are heterogeneous, species-specific, and the severity of the impacts depends on the identity of the invading plant species (e.g. Hejda et al. 2009, Vilà et al. 2011).
Generally, agricultural habitats are regarded as vulnerable to plant invasions but the invasion level varies among agricultural habitat types (e.g. Chytrý et al. 2005, Vilà et al. 2007, Pyšek et al. 2009a). Frequently disturbed and more intensively managed agricultural habitats, such as arable land, field and road margins within agricultural landscape, are more often invaded by the alien plant species than infrequently disturbed and less intensively managed agricultural habitats, such as grasslands (I, see also e.g. Chytrý et al. 2005, Pyšek et al. 2009a, 2010). Thus, in agricultural landscape the control and management of alien plant species should be targeted to these frequently disturbed habitats in order to prevent invasions to undisturbed natural habitats. In addition, propagule pressure and management strategies, which increase the disturbance intensity and/or frequency, should be limited to prevent the establishment of the alien plant species (e.g. Hobbs and Huenneke 1992, Cole et al. 2007). I did not found evidence that mowing as a control method would decrease alien species richness. This may be caused by the low intensity of mowing. In most of the study sites, the mowing had been conducted only once as part of the management of field or meadow, and not targeted for controlling alien plant species. Mowing might control dominant grasses (Hobbs and Huenneke 1992), and increase native plant species diversity at semi-natural grasslands and field margins in Scandinavia (e.g. Hovd and Skogen 2005, Pykälä 2007, Tarmi et al. 2011). When mowing is performed in optimum flowering stage and repeated several times, it may be suitable and efficient method to control invasive alien plant species (e.g. DiTomaso 2000, Wilson and Clark 2001, Valtonen et al. 2006).

Currently, it generally appears that alien plant species do not cause severe problems on native species diversity in Finnish semi-natural agricultural habitats although alien species are known to have harmful effects on native species in other habitat types (e.g. Valtonen et al. 2006, MMM 2012). In addition, the most harmful invasive alien species, such as *Heracleum mantegazzianum* have not yet invaded semi-natural agricultural habitats (II). However, my assessments of the impact of alien plant species were directed only to the native species richness and diversity, and concerned only the most common neophytes of the agricultural habitats. Many invasive alien plants are known to cause multiple impacts, but the current understanding is often restricted to relatively few dominant species (e.g. Pyšek et al. 2008, Vilà et al. 2011), and the impacts of the great majority of the alien species have never been studied (Simberloff 2011). Although in the Finland’s a National Strategy on Invasive Alien Species (MMM 2012) invasive alien plant species (i.e. those species which threaten native diversity and ecosystems or cause economic, health and
social hazards) of Finland were assessed, studies of the ecological impact of alien plant species are still lacking from Finland (but see Valtonen et al. 2006, Ramula and Pihlaja 2012). Further study of the ecological impacts of both dominant and less dominant alien plant species in the Finnish agricultural habitats is needed due to context-dependence in the magnitude of the impact and direction of the ecological change (Vilà et al. 2011), and also for the implementation of the National Strategy on Invasive Alien Species in Finland. However, at the moment, there is no need to focus primarily on agricultural habitats, when implementing the National Strategy on Invasive Alien Species in Finland. Future studies should include the impacts at species, community and ecosystem level, and consider also the impacts on higher trophic levels, ecosystem services and agriculture as a whole (e.g. Vilà et al. 2010, 2011).

I used invasion level of alien plants to assess the extent or severity of alien species invasion, and to reveal spatio-temporal trends in invasion level in different semi-natural agricultural habitats and in different geographical regions of Finland (I, II). However, invasion level does not reveal whether or not, and to what extent certain habitat is prone to invasion (e.g. Pyšek et al. 2010a). Hence, my studies did not consider invasibility, that is, habitat's inherent susceptibility to invasion (e.g. Lonsdale 1999, Richardson et al. 2011). Invasibility can be characterized by the survival rate of invading species when the effects of propagule pressure and confounding effects such as climate are held constant (e.g. Chytrý et al. 2008a, Catford et al. 2012). So, in order to understand why some habitats are more invaded than others, the effects of habitat properties should be separated from the effects of propagule pressure and other confounding factors (e.g. Chytrý et al. 2008a, Pyšek et al. 2010a). Invasibility has rarely been quantified, possibly due to difficulties in measuring propagule pressure (e.g. Eschtruth and Battles 2011, Catford et al. 2012).

Propagule pressure is a fundamental determinant of invasion level (e.g. Colautti et al. 2006), crucial in understanding plant invasions (e.g. Lockwood et al. 2005, Simberloff 2009), and the absent of variables related to propagule pressure is a substantive deficiency in this thesis. For instance, propagule pressure may contribute to the positive diversity-invasibility relationships (III) (e.g. Levine 2000, Fridley et al. 2007, Eschtruth and Battles 2011). For a comprehensive data set as the one used in this study, it is very time-consuming and almost impossible to measure propagule pressure as the naturally occurring levels of propagules (e.g. number of seeds or seedlings) (see e.g. Eschtruth and Battles 2011). Though the use of proxies for propagule pressure (e.g. human population density or distance from a river or an urban area) does not quantify the actual levels of propagules, it should be taken into account in the future studies of invasibility and invasion level (e.g. Chytrý et al. 2008a, Eschtruth and Battles 2011). Another deficiency in this thesis is the lack of socioeconomic and demographic variables, which reflect the
intensity of human activities, such as trade and transportation (e.g. Pyšek et al. 2010b). Human activities are considered as an important predictor of plant invasions (e.g. Essl et al. 2011), and the inclusion of such variables would have been justified especially at larger spatial scale.

The results of my thesis highlight the fact that characteristics of the alien plant species and their preferences for environmental conditions are species-specific. In addition, alien species impacts on native species and ecosystems are heterogeneous and species-specific (II), and the severity of the impact depends on the features of the invading species (e.g. Hejda et al. 2009, Vilà et al. 2011). However, all alien species do not possess a threat to native species diversity (see e.g. Davis et al. 2011) (II), and alien species may indicate disturbance and land-use change rather than direct threat to biodiversity (Maskell et al. 2006). Therefore, management and control strategies should be considered case-by-case, taking into account local environmental conditions and characteristics of the invading species (IV), including their preferences for environmental conditions (II). In addition, the invasion patterns and processes, such as dispersal, diversity-invasibility relationship, and the ecological impacts of plant invasions are greatly influenced by the spatial scale (e.g. Pauchard and Shea 2006). Thus, plant invasions are highly complex and there is no generalization for ideal plant invader that could be applied in different environmental conditions worldwide (IV, e.g. Alpert et al. 2000, Richardson and Pyšek 2006). Although plant invasions are species-specific, it is possible to explain the occurrence and establishment of alien species by a combination of environmental characteristics, life-history traits and invasion history (IV). This information is useful to extend our understanding of the most successful alien plant species in agricultural habitats, and our ability to predict the spread of these species (IV). In addition, comprehensive, habitat-specific studies on the determinants of occurrence of alien plant species at multiple spatial scales are important for developing a deeper understanding of the patterns of invasions.

In this study, I used a comprehensive data, which was originally collected for national monitoring of the effects of the Finnish agri-environmental support scheme (Kuussaari et al. 2008). This data provides a unique, comprehensive insight of the spatio-temporal variation in plant diversity and the invasion level of alien plants in Finnish agricultural habitats. However, the random sampling design and patchy occurrence of invasion alien species may lead to underestimation of harmful effects of alien plant species at local spatial scale on species occurring at low frequency and species occurring in habitats not covered by the sampling e.g. gardens (see e.g. Lampinen and Lahti 2011). In addition to the comprehensive sampling data, a survey on the most infested sites invaded by worst invasive plant species is needed to evaluate the conditions of these sites. In addition, the environmental variables of the data set were problematic, because most of them were visually assessed or on ordinal scales, not measured exactly on continuous, absolute scales (e.g.
coverage of bare ground, moisture). In addition, many environmental variables (e.g. coverage of bare ground and total vegetation) correlated strongly with the plant data and each other, because they were based on coverage estimation from the same study plot. Especially, inclusion of edaphic variables, such as nitrogen level and moisture, and more detailed information of management, land-use and farming type (e.g. organic vs. conventional) would enhance the quality of the data set. In addition, the temporal scale consisted only three separate years during one decade, thus the changes in invasion level and occurrence of alien plant species may reflect stochastic variation in the environmental variables. In order to detect the actual variation in invasion level and reveal reliable trends in invasion level though space and time, a longer monitoring period is needed.

My results provide a comprehensive overview on the occurrence of alien plant species in Finnish agricultural habitats, and of the abiotic and biotic factors affecting the invasion level and the occurrence of alien plant species. The patterns and processes of plant invasion are highly complex, species-specific and dependent on the habitat characteristics. There is no simple, single solution to control invasive alien plant species. Thus, the estimations of the impact of alien plant species and the management strategies should be species-specific, taking into account the features of the invading plant and the environmental characteristics. In the future, comprehensive, habitat-specific studies on the determinants of occurrence of alien plant species at multiple spatial scales are needed for developing a deeper understanding of the patterns of invasions. These studies should include an estimation of propagule pressure and an assessment of ecological impacts of invasive alien plant species at multiple levels.
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