Eesti Maaülikool
Estonian University of Life Sciences

DISTRIBUTION AND HABITAT PREFERENCES OF THE CLOUDED APOLLO BUTTERFLY [PARNASSIUS MNEMOSYNE (L.)] IN ESTONIA

MUSTLAIK-APOLLO [PARNASSIUS MNEMOSYNE (L.)] LEVIK JA ELUPAIGA EELISTUSED EESTIS

KADRI KASK

A Thesis
for applying for the degree of Doctor of Philosophy
in Environmental protection

Väitekiri
filosoofiadoktori kraadi taotlemiseks keskkonnakaitse erialal

Tartu 2015

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following articles, which are referred to in the text by their Roman numerals.

I. Liivamägi, A., Kuusemets, V., Luig, J. & **Kask, K**. 2013. Changes in the distribution of Clouded Apollo *Parnassius mnemosyne* (Lepidoptera: Papilionidae) in Estonia. Entomologica Fennica 24(3): 186–192.

II. **Meier, K**., Kuusemets, V., Luig, J. & Mander, Ü. 2005. Riparian buffer zones as elements of ecological networks: Case study on *Parnassius mnemosyne* distribution in Estonia. Ecological Engineering 24: 531–537.

III. Kuusemets, V., **Kask, K.,** Liivamägi, A., Luig, J., Kaart, T., Kull, A. & Kull, A. The habitat preferences and range expansion of the Clouded Apollo butterfly *Parnassius mnemosyne* (L.) in Estonia. Submitted.

IV. **Meier, K.,** Kuusemets, V. & Mander, Ü. 2005. Socio-economic and land-use changes in the Pedja River catchment area, Estonia. In: River Basin Management III. WIT Transactions on Ecology and the Environment. WIT Press. Vol 83: 585–592.

Contributions:

	I	II	III	IV
Idea and study design	KK, VK, AL, JL	VK, JL, ÜM	KK, VK, AL	VK, ÜM
Data collection	KK, VK, AL, JL	KK, VK, JL	KK, VK, AL, JL	KK, VK
Analysis of data	KK, VK, AL	KK, VK, JL	TK, KK, AiK, AnK, VK, AL	KK, VK
Manuscript preparation	VK, AL	KK, VK, ÜM	KK, VK, AL	KK, VK, ÜM

TK – Tanel Kaart; KK – Kadri Kask (former name Kadri Meier); AiK – Ain Kull; AnK – Anne Kull; VK – Valdo Kuusemets; AL – Ave Liivamägi; JL – Jaan Luig; ÜM – Ülo Mander.

1. INTRODUCTION

According to the European Red List of Butterflies, 31% of European butterflies have declining populations, and approximately 9% are threatened (van Swaay et al. 2010). The grassland specialist species have declined more rapidly compared with other species (van Swaay et al. 2006). One of the specialist butterfly species that has a declining population throughout Europe and that has been of interest to many scientists, is the Clouded Apollo [(*Parnassius mnemosyne* (L.)]. The distribution and abundance of the Clouded Apollo has been reported to be in decline in Central Europe (Meglécz et al. 1999, Konvička & Kuras 1999), and in northern Europe in Norway (Aagaard et al. 2009), Sweden (Franzen & Imby 2008), and Finland (Välimäki & Itämies 2005). According to IUCN Red List criteria, the Clouded Apollo has experienced a decline in area of occupancy, extent of occurrence and/or quality of habitat (van Swaay et al. 2010). Therefore, the species is strictly protected by the Bern Convention (Annex II), by the EU Habitat Directive Natura 2000 (CEE Habitat Directive 43/92, Annex IV), by several national protection acts and is included in the European Red List of Butterflies as a near threatened species, as well as many regional Red Data Books. In Estonia, the butterfly has been under legal protection since 1995 and, by government regulation (No. 195, 20.05.2004), presently has category II protection.

The primary reason for the decline of butterfly populations has been the abandonment of extensive agricultural areas, brought on by socio-economic changes, and resulting in the overgrowth of suitable habitats. Similarly, habitats of the Clouded Apollo have been affected by the termination of traditional management, such as grazing and mowing of semi-natural grasslands (Bolotov et al. 2013), leading to habitat loss and fragmentation (Välimäki & Itämies 2003). In Estonia, as in other European countries, extensive traditional agricultural practice is decreasing, resulting in the loss of such habitats (Kukk & Sammul 2006).

Despite this trend, the area of semi-natural grassland that is suitable habitat for the Clouded Apollo remains high, and increasing occupancy by the Clouded Apollo has been observed in recent decades within Estonia. Therefore, there is a high degree of interest in the scientific study of the species.

2. REVIEW OF THE LITERATURE

2.1. Biology of the Clouded Apollo

The Clouded Apollo (*Parnassius mnemosyne* Linnaeus, 1758) is a white swallowtail butterfly (Papilionidae, Lepidoptera) with two black costal spots and a broad semi-transparent margin on the forewing, a broad black inner margin; and often a black discal spot on hind-wing (Lafranchis 2004; Figure 1).

The butterfly is a univoltine species that hibernates as a larva inside the egg. After snow melt in April, the larvae hatch from the eggs and begin to look for food plants, which begin to grow at the same time (Viidalepp 2000). The larvae of the Clouded Apollo are monophagous on the plant genus *Corydalis* (Papaveraceae). In southern and Central Europe, the Clouded Apollo feeds on *Corydalis cava, C. solida, C. fabacea,* and *C. pumilla* (Maglécz et al. 1999, Konvička et al. 2007); in Sweden, on *C. intermedia* and *C. pumila* (Franzén & Imby 2008); in Norway, on *C. intermedia* (Aagaard et al. 2009); in Finland, on *C. solida* (Luoto et al. 2001); and in Russia, on *C. solida* and *C. capnoides* (Bolotov et al. 2013). In Estonia, the larvae feed on the leaves of *C. solida*. *C. intermedia* is also found in Estonia, but its distribution is very limited, and there are no reports of Clouded Apollo larvae on *C. intermedia* in Estonia. The primary

Figure 1. The imago (left) and the larva (right) of Clouded Apollo (photos V. Kuusemets)

nectar plants of the adults are *Geranium* spp., *Viscaria vulgaris*, *Anchusa officinalis*, *Knautia arvensis* and *Glechoma hederacea* (Viidalepp 2000).

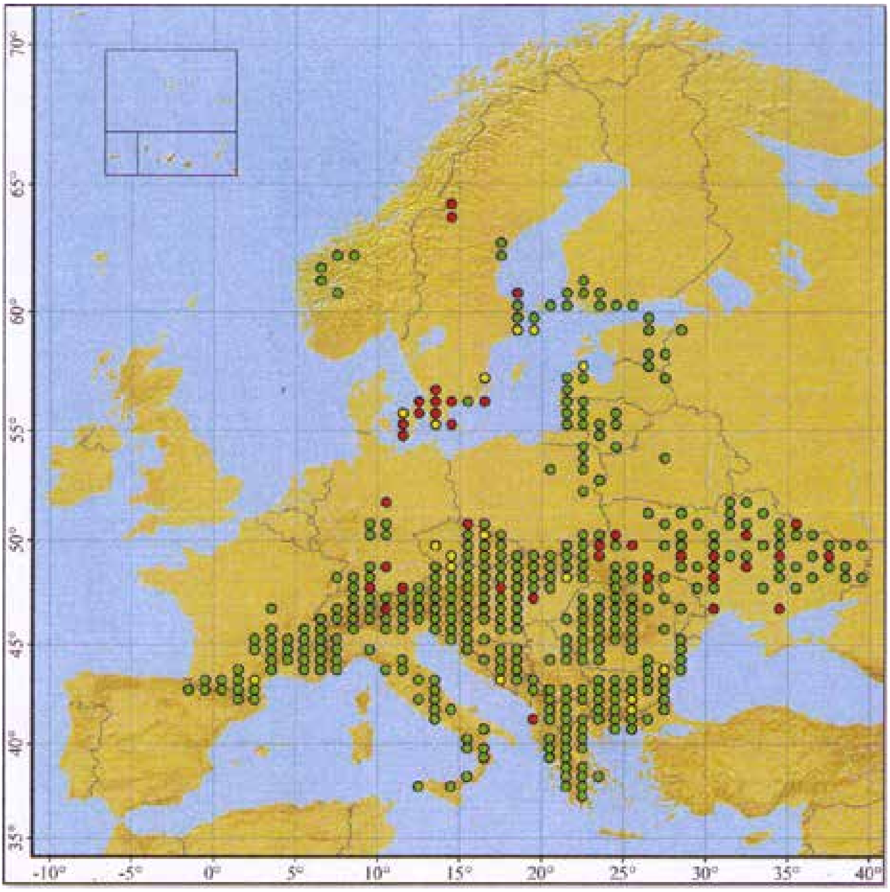
The butterfly uses open meadows for mating; during copulation, the male attaches a special mating plug, called a sphragis, to the ventral side of female's abdomen. The purpose of the sphragis is to prevent copulation by other males. However, some females may lack a sphragis after mating (Vlasanek & Konvička 2009). At the time of oviposition, the food plants of the larvae have no aboveground structures. Recent studies have shown that the female actively oviposits in open clearings near plant bulbs, which she locates using existing vegetation, such as shrubs (Konvička & Kuras 1999, Bergström 2005).

2.2. Distribution of the Clouded Apollo

The Clouded Apollo is a Western Palearctic species (Gorbach & Kabanen 2010). It is distributed in isolated colonies from northern Spain throughout most of Europe, and eastwards to the Caucasus, western Russia, and Central Asia (Kudrna et al. 2011, Bolotov et al. 2013; Fig 2). The Clouded Apollo generally inhabits heterogeneous environments with small isolated habitat patches (Välimäki & Itämies 2003, Gorbach & Kabanen 2010) that are typical of metapopulations (Hanski & Thomas 1994). In Scandinavia, the butterfly is found in discrete subpopulations and has a naturally fragmented distribution (Franzén & Imby 2008, Aagaard et al. 2009). In Estonia, there are three isolated populations, each with a different subspecies: *P. mnemosyne osiliensis* (Bryk 1922) on Saaremaa Island, *P. mnemosyne estonicus* (Viidalepp 2000) in northeastern Estonia, and *P. mnemosyne viidaleppi* (Kesküla & Luig 1997) in South Estonia. The Saaremaa population is probably extinct; although many entomologists have searched for the butterfly in this area, the last sighting of the butterfly was in 1973 (Viidalepp 2000). In the other two regions of Estonia, the Clouded Apollo has expanded its distribution.

The geographic distribution of the Clouded Apollo generally coincides with the distribution of its host plant, which is relatively fragmented. The Clouded Apollo is believed to be a sedentary species with poor dispersal that moves relatively short distances (Konvička & Kuras 1999, Meglécz et al. 1999, Välimäki & Itämies 2003, Gorbach & Kabanen 2010). This combination of specific habitat requirements and limited movement makes colonisation of new areas difficult for the species.

Parnassius mnemosyne (Linnaeus, 1758)



Zoogeography: From N. Spain in isolated colonies through most of Europe eastwards to Caucasus and C. Asia. – ZS: Euro-Oriental species.
Conservarion: RA 2. – BRF 408. – DI 21.93 %. – IUCN RL 2010: Europe NT, EU27 LC. – FFH 93/43: IV. – CRAEB: HR.

Figure 2. The distribution of the Clouded Apollo in Europe (Kudrna et al. 2011).

2.3. Habitat preferences of the Clouded Apollo

The Clouded Apollo inhabits different biotopes within its distribution. In southern Europe, the Caucasus and the mountainous areas of Central Europe, the butterfly is typically found on damp to moderately dry grasslands at higher elevations, usually near woodlands or scrub (Viidalepp 2000, Settele et al. 2008). In areas of Central Europe with lower elevation and less relief, the butterfly is found in sparse deciduous forests, forest clearings and at the sunny margins of humid, deciduous forests

(Meglécz et al. 1999, Konvička & Kuras 1999). In the northern part of the distribution, the butterfly is found in river valleys with semi-natural grasslands (Luoto et al. 2001, Bolotov et al. 2013). In Norway and Sweden, the butterfly is found primarily along the coast. However, in Norway, the Clouded Apollo is also found in open mountain meadows (Aagaard et al. 2009), and in Sweden, it is also found in areas with a mosaic of deciduous forest and scrubby meadow verges (Franzén & Imby 2008).

This butterfly has very complex requirements for the larvae and the imago, and therefore needs a well-structured habitat (Konvička & Kuras 1999). The primary habitat requirements of butterflies in general, and the Clouded Apollo in particular, are first, nectar sources. Several studies have found that the abundance and species richness of butterflies is dependent on the abundance and richness of nectar plants (Luoto et al. 2001, Pywell et al. 2004). Second, suitable sites are required for mating and oviposition (Välimäki & Itämies 2003, Bergström 2005). Third, suitable food plants are required; as the larvae of the Clouded Apollo are monophagous on *Corydalis spp.,* the butterfly is dependent on the food plant of the larvae (Konvička & Kuras 1999, Luoto et al. 2001, Bergström 2005). Fourth, shelter is required; as a large butterfly with low mobility, the Clouded Apollo needs the shelter against the wind (Dover et al. 1997, Pywell et al. 2004, Rosin et al. 2012). Fifth, optimal patch size is needed. In general, the abundance of butterflies increases with patch size (Krauss et al. 2003, Öckinger et al. 2012). However, different species may require different patch sizes, especially specialist species (Dover & Settele 2009, Rosin et al. 2012), such as the Clouded Apollo.

2.4. Influence of landscape patterns on butterflies

Several studies illustrate the importance of landscape structure and connecting corridors on the movement of butterflies (Dover et al. 1997, Haddad 1999, Brückmann et al. 2010, Öckinger et al. 2012). In landscape ecology, the landscape structure is composed of the matrix and landscape elements within the matrix (Forman & Gordon 1986). The matrix is the dominant background ecosystem, such as a forest. In population ecology, the most important landscape elements are patches, polygonal elements that delineate habitats for species, and corridors with stepping stones or strips for species movement across landscapes and barriers (Naiman et al. 2005). The territorial ecological network is a hierarchical system with the following levels: (1) core areas; (2) buffer zones around core areas, corridors and stepping stones; and (3) nature development and/or restoration areas that support resources, habitats and species (Baldock et al. 1993). Protected areas are classified as core areas within ecological networks, whereas the areas suitable for ecological networks can be considered buffer zones and/or corridors.

One natural form of corridor is the riparian area along rivers (Naiman et al. 2005). Rivers, with their tributaries, create a natural system of "veins" which constitute natural corridors through different communities and ecosystems, providing connectivity among core areas. For this reason, riparian areas may be of interest in butterfly studies. However, few investigations have been conducted on the use of riparian areas by butterflies.

2.5. Influence of socio-economic factors on habitat change

The primary habitat of the Clouded Apollo—semi-natural meadows—is correlated with extensive traditional agriculture in Estonia. Significant changes have occurred in land use throughout the century, and these agricultural changes have often been associated with political and socio-economic changes. In Estonia, significant changes took place during and after the Second World War. Extensive traditional agriculture was replaced by intensive cultivation in large fields, and small fields became overgrown. Another significant change took place after the re-establishment of Estonian independence in 1991. Many agricultural areas were set aside, and the abandonment of marginal semi-natural habitats increased. The area of semi-natural grasslands in Estonia has decreased substantially—from 1,571,000 ha in 1939 to 130,000 ha in 2006 (Kukk & Sammul 2006). This decrease is primarily due to grasslands being overgrown by forests; the area of forest has increased almost threefold from 1940 to 2000 (Mander & Palang 1999, Kaasik et al. 2011). The overgrowth of suitable habitats is one of the primary threats to the Clouded Apollo (Välimäki & Itämies 2003, Bolotov et al. 2013), and requires special attention to protect the species.

3. AIM OF THE THESIS

The abundance, distribution, changes in distribution, and the reasons for these changes have not been well-analysed for Estonian butterflies. In particular, protected species in need of attention should be carefully studied, and their populations, distribution changes, and habitat preferences, should be clarified to develop appropriate protection and management strategies that will ensure the preservation of the species.

The main hypotheses of the study were:

- The abundance and distribution range of the Clouded Apollo have increased during recent decades in Estonia (Paper I);
- The abundance and distribution range of the Clouded Apollo has increased due to the high habitat quality and due to the suitable landscape structure in Estonia (Paper II and Paper III);
- The socio-economic changes can lead to the fast loss of the valuable semi-natural habitats (Paper IV).

The aim of the thesis was:

- To study the abundance and distribution of the Clouded Apollo throughout the period of available observations and to analyse its changes in Estonia (Paper I);
- To determine the habitat preferences of the Clouded Apollo in Estonia (Paper II and Paper III);
- To analyse the effect of landscape elements on the distribution of the Clouded Apollo (Paper II and Paper III);
- To evaluate socio-economic changes, and land use changes of semi-natural meadows during last 50 years, using the example of the Pedja River riparian area (Paper IV).

4. MATERIALS AND METHODS

4.1. Database creation for the Clouded Apollo (Papers I and III)

We studied the distribution of the Clouded Apollo in three steps, first for period 1903–2003 (Paper II), and later using the updated database (Paper I) for the period 1878–2010. Finally, we summarised all known sightings of the butterfly through the end of 2014. We collected all known records of Clouded Apollo sightings in Estonia. The records of sightings were collected from various sources, such as the national periodical publication *Lepinfo*, issued by the Estonian Lepidopterologists' Society, and the entomology section of the Estonian Naturalists' Society, which has published most sightings of butterflies since 1981 in Estonia. In addition, data were collected from two major butterfly collections in Estonia—the Natural History Museum of the University of Tartu; and the entomology collection of the Department of Zoology, Institute of Agricultural and Environmental Sciences, at the Estonian University of Life Sciences. Many data from earlier periods, and data that were not published in *Lepinfo*, were gathered directly from entomologists. In addition, several records were acquired from the literature and from researchers and local surveys of the butterfly. Finally, data from our own fieldwork during the period 2002–2012 were added to the database. We determined geographic positions of the descriptions and sightings of butterflies, and created a common GIS database using MapInfo Professional 9.0 and 10.0.

The data were gathered by different groups of people (qualified lepidopterists, amateur lepidopterists, and volunteers), and therefore the data have variable accuracy. Most of the earlier records were more general, providing the name or the description of the location using landmark features such as roads, rivers, and bus stops. The accuracy of these data are within several kilometres, but at least within 5 km. The data of *Lepinfo* are given in UTM coordinates, which uses a 10 x 10 km grid system, and give the name of the location of the sighting. In most cases, the location of the sighting accurately describes specific patches or habitats of the butterfly, and therefore the accuracy of the *Lepinfo* data are assessed at within 1 km. Records of entomologists and researchers from later periods (since approximately 2000) and our own field work records have been fixed using portable GPS units, or a basic map (1:10,000) that gives the exact position of the butterfly with an accuracy of tenths of meters.

Although the accuracy of the data differs among different data sets, it is adequate for analysing the species distribution at the scale of the entire country during the long period (134 years) since the first record of the Clouded Apollo in Estonia.

All descriptions of butterfly sightings were linked with a digital cadastral or basic map of Estonia (1:10,000) to the common GIS database using MapInfo Professional 9.0 and 10.0. The Clouded Apollo database consists of data on the exact location of the sightings (place name, or coordinates if possible); the level of accuracy on a scale of 1–3 (1: exact location, 2: grid system coordinates, 3: descriptive location); date and time of the observation; name of the observer; number and gender of butterflies, if determined and counted; source of the data and a short description of the habitat. For analyses of distribution changes over time (Paper I), we divided our data into five study periods: 1878–1969, 1970–1979, 1980–1989, 1990–1999 and 2000–2010. The first period is longer than the other periods because there were only isolated records of the butterfly during these years. For study of the South Estonian population (Paper III), data were used from the period 1984 to 2012.

4.2. Habitat and landscape studies (Papers II and III)

The habitat study was carried out in the largest subpopulations of the butterfly, in the central Ahja River valley and in the Piusa River valley. We described the mapped distribution of *Corydalis solida* near the subpopulations at the end of April and beginning of May of 2004 and 2005, during the period of most active flowering of the plant. Both banks and their surrounding areas were checked continuously, and all observations of the flowers were recorded on the map and included in the GIS database. The abundance of Clouded Apollo butterflies on habitat patches was determined during the first half of June at approximately midday, on days with sunny weather, temperatures greater than 16° C and wind speeds of less than three on the Beaufort scale. The number of Clouded Apollos was counted, and the type of habitat patch was described for the Ahja River subpopulation (total n=17; for statistical analysis, one outlying patch was removed, giving n=16).

Table 1. Values for openness and surface roughness of CORINE land cover classes (Kull 1996).

Openness value	Code and name of CORINE land cover classes		Roughness value
0–0.2	4111	Inland marshes	0.1
	4122	Natural peat bogs with scattered trees and shrubs	0.03
	321	Natural grasslands	0.1
	211	Non-irrigated arable land	0.1
	4112	Open fens and transitional bogs	0.03
	231	Pastures	0.1
	122	Road and rail network	0.1
	333	Sparsely vegetated areas	0.05
	4121	Explored peat bogs	0.01
	512	Water bodies	0
	511	Water courses	0
0.2–0.4	334	Burnt areas	0.3
	242	Complex cultivation patterns	0.3
	133	Construction sites	0.3
	132	Dump sites	0.3
0.4–0.6	112	Discontinuous urban development	0.5
	222	Gardens	0.5
	121	Industrial or commercial units	0.5
	243	Land principally occupied by agriculture	0.5
	322	Moors and heathland	0.5
	3241	Transitional woodland /scrub on mineral soil	0.5
	3242	Transitional wood-land/scrub on mire	0.5
0.6–0.8	311	Broad-leaved forest	0.7
	141	Green urban areas	0.7
	142	Sport and leisure facilities	0.6
0.8–1.0	312	Coniferous forest	1
	111	Continuous urban development	1
	313	Mixed forest	0.8

The butterfly was found in 3 types of habitat: dry semi-natural meadows, dry semi-natural meadows with a strip of trees and wet meadows with a strip of trees. The semi-natural meadows studied were species-rich, with several flowering species that were good nectar sources for the butterflies.

We calculated the area (ha) and perimeter (m) of patches from the Estonian digital basic map (1:10,000) provided by the Estonian Land Board. We used single-factor dispersion analyses and regression modelling to determine if there was any statistically significant relationship between meadow patch area/perimeter and the abundance of Clouded Apollos. The analyses were performed using the statistical software STATISTICA 9; significance was assigned at $p < 0.05$.

In both subpopulations of Clouded Apollo, Ahja River valley and Piusa River valley, the vertical structure of the surrounding land cover types was assessed by the openness of surrounding landscapes. We used a digital CORINE land cover map (1:100,000) as a more generalised land cover map available for all of Estonia, and assigned 'openness values' to the different land cover types surrounding butterfly habitats. We determined surface roughness values, which are used to assess wind speed in different biotopes and are based on the height of vegetation (Troen & Petersen, 1989), and transferred them to the CORINE land cover classes (Kull 1996). Using surface roughness, we divided land cover types into 5 classes where lower values (<0.2) indicated more open areas (e.g., grasslands) and higher values (0.8–1.0) indicated taller, closed areas (e.g., coniferous forest, Table 1). Using the assigned classes, a map of the openness of land cover types adjacent to the habitats of Clouded Apollos was created using MapInfo Professional 10.0.

Finally, in all subpopulations where the exact position of butterflies was known, we calculated the average distance of butterflies from water bodies, with an accuracy of 5 m.

4.3. Socio-economic and land cover changes (Paper IV)

Analysis of socio-economic changes were conducted for the landscapes surrounding the Puurmani community and the Pedja River. We used the database of the Statistical Office of Estonia (SOA). The analysis of land use changes were conducted by comparing Estonian cadastral maps from the 1930s with maps from the early 1990s.

The Puurmani community is situated in central Estonia, in southwestern Jõgeva County. The area of the community is 292.7 km^2, which is slightly larger than the average area of Estonian rural municipalities (212 km^2). The central village of the rural municipality, Puurmani, is situated

27 km from the county centre (Jõgeva), and 38 km from the second largest town in Estonia (Tartu).

Most of the soils are humid or wet and are suitable for agriculture only after drainage. In the western part of the community, there is a large wetland system surrounding the Pedja River valley that, from 1952 until 1991, was used for bombing practice by the Soviet Air Force. In 1994, the Alam-Pedja Nature Reserve was established in this area, and it is included in the list of Ramsar sites. The total area of the reserve is 260 km^2, 82% of which is wetland. The Emajõgi, Pedja and Põltsamaa rivers flow through the protected area; the flooded area in springtime can reach 92 km^2, which creates valuable habitat of European importance. The rivers have flooded meadows on their banks that have historically been extensively cultivated, and constitute species-rich meadows of high ecological value.

5. RESULTS

5.1. Distribution changes of the Clouded Apollo (Papers I and III)

We studied the distribution of the Clouded Apollo in two steps, first for the period 1903–2003 (Paper II), and later using the updated database (Paper I) for the period 1878–2010. In the first study, we examined the results of 116 records and found that 73% of sightings were from 1990 or later, and only 16% of sightings were from 1980 or earlier. In the second study, several of our own sightings were included in the database, and the number of unique locations and records analysed was 307. Therefore, the record of distribution changes is more accurate and covers a longer period in Paper I.

The first record of *P. mnemosyne* is from 1878 in Northeast Estonia. In 1922, the butterfly was discovered on the island of Saaremaa, and in 1984, it was discovered in Southeast Estonia.

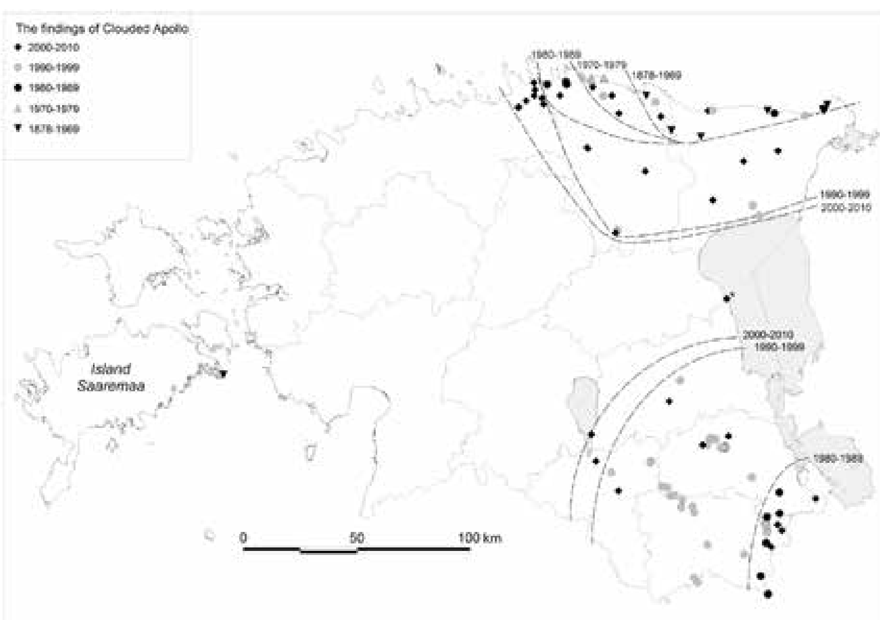


Figure 3. Distribution of the Clouded Apollo in Estonia from 1878–2010. The broken lines show the extent of the butterfly distribution during a given period. The record with an asterisk (*) concerns a single findings from the year 2002 (five individuals). Therefore, the 2000–2010 line was not drawn to include this record.

Most records of sightings (82%) are from 1980 or later. Only 18% of all records are from the first 100-year period, from 1878–1979. There are 41 records of the Clouded Apollo from the first study period, 1878–1969, primarily from eight locations in Northeast Estonia, and only one location (Kübassaare) on the island of Saaremaa. Between 1970 and 1979, there are 13 records, the majority of which are located in Northeast Estonia, with one on the island of Saaremaa. During the period 1980–1989, there are 32 records in Estonia; the butterfly was recorded 19 times in Northeast Estonia and 13 times in South Estonia. Within the periods 1990–1999 and 2000–2010, the number of records increased to 95 and 126, respectively. Approximately two-thirds of the sightings from the last two study periods are located in South Estonia, where the number of recorded individuals has reached 300.

Changes in the distribution of the Clouded Apollo in Estonia are shown in Figure 3. During the period 1878–1969, the distribution of the butterfly remained local in Northeast Estonia. During the periods 1970–1979 and 1980–1989, the species moved westward, with a maximum decennial expansion distance of approximately 30 km and 20 km, respectively. During the last two decades (1990–1999 and 2000–2010), the range expansion of the butterfly has continued to move to the west and the south.

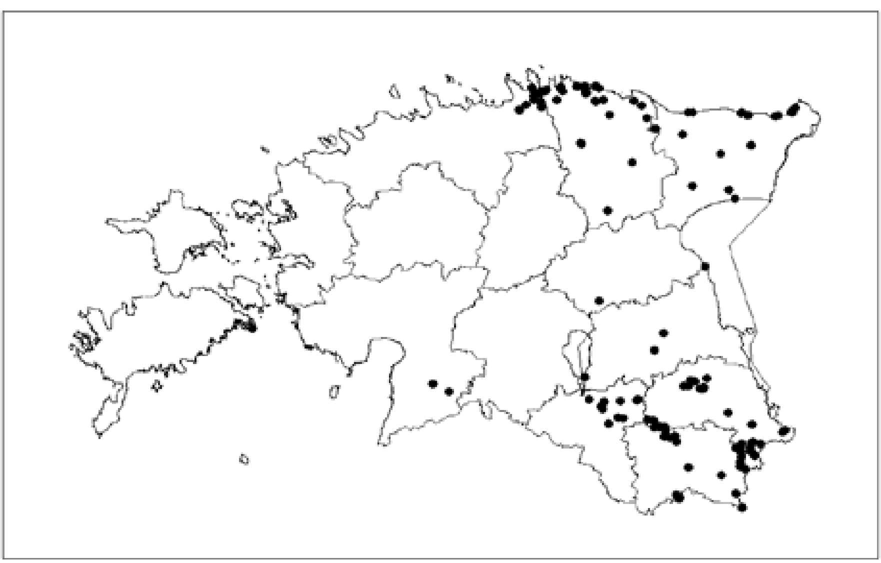


Figure 4. All sightings of the Clouded Apollo in Estonia through 2014.

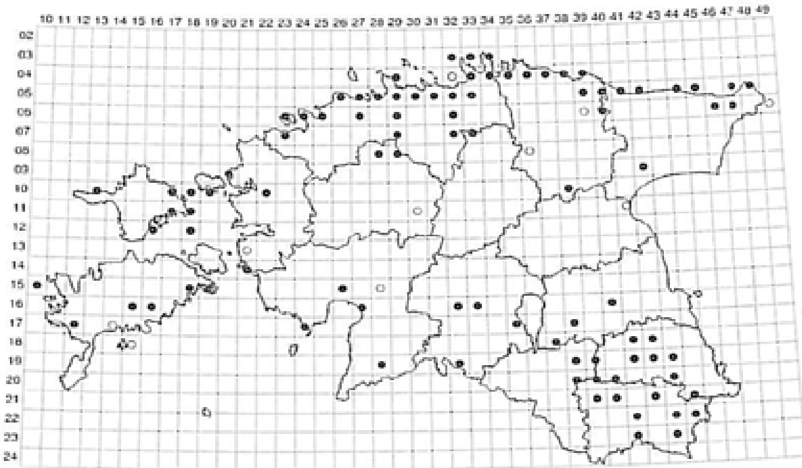


Figure 5. The distribution of *Corydalis solida* in Estonia from 1921–2005 displayed on a grid of 9 × 11 km squares. Empty circle: recorded from 1921–1970; filled circle: recorded from 1971–2005 (Kukk & Kull 2005).v

On the island of Saaremaa, the butterfly was found during the period 1922–1973, but it remained local and few in number in its habitats throughout the entire period. The butterfly has not been observed there since 1973, despite continuous visits by entomologists to these habitats and is likely extinct.

In Southeast Estonia, the butterfly was first recorded in 1984 near the Pedetsi and Piusa Rivers. Six years later, the butterfly was already found approximately 40 km to the northwest in the Ahja River valley, and after an additional five years, was found approximately 55 km to the west in the Võhandu River valley. Over a ten-year period from 1984 to 1993, the Clouded Apollo migrated up to 75 km westward to the Puka region (Figure 9).

However, during the years since the publication of Paper I, new sightings of the butterfly have been recorded in southwestern Estonia near Kilingi-Nõmme, where a subpopulation was established and was still found several years later. Similarly, the location of sightings near Mustvee that were marked on the previous map as a single record (the sighting with the asterisk in Figure 3) has become a significant subpopulation during recent years. Therefore, an additional map of sightings of the Clouded Apollo was created, showing all known sightings through 2014 (Figure 4).

The butterfly is monophagous and therefore is dependent on its food plant. Hence, the distribution pattern of the Clouded Apollo is generally consistent with the distribution of its larval host plant, fumewort (*Corydalis solida*). The distributions are similar and the butterfly is found almost in all locations where the host plant fumewort has been found (Figures 4 and 5). Only in western Estonia has the butterfly not yet been found. Sightings of the butterfly are also in very good agreement with the sightings of fumewort in the landscape study (Figure 10).

5.2. Habitat preferences of the Clouded Apollo (Papers II and III)

Our first study (paper II) showed that the Clouded Apollo was found on the shores of lakes (13% of all sightings), in the coastal areas of the Baltic Sea (9%) and the especially on the banks of rivers (78%). The landscape study showed that the Clouded Apollo was primarily associated with dry riparian meadows on the banks of rivers with a strip of alders (*Alnus incana*); the butterfly populated 13 of 17 habitats of this type. The typical density of butterflies was between 51 and 100 individuals per hectare, with up to 200 individuals per hectare in the three meadows with an alder strip. In four cases, the Clouded Apollo was found in wet meadows.

The Clouded Apollo was primarily observed flying close to water bodies with a riparian strip of alders (Paper III). The butterfly was typically

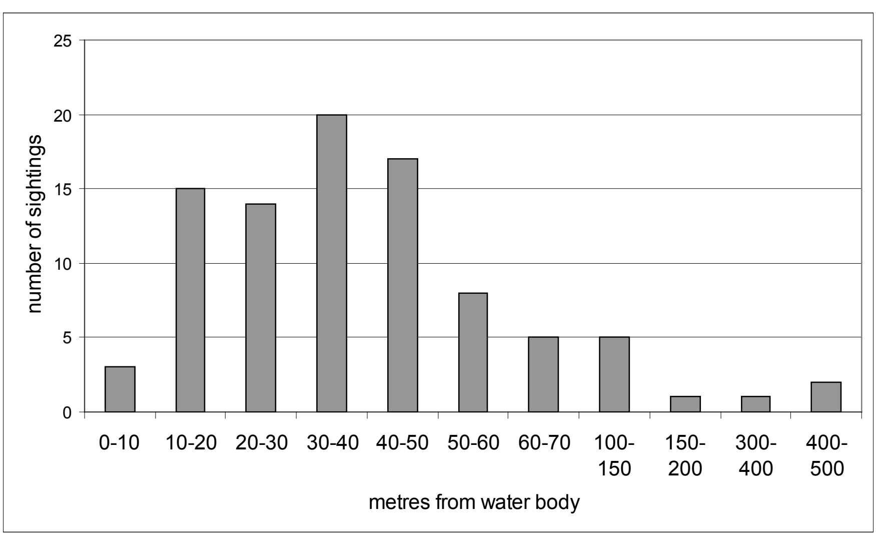


Figure 6. Distances of Clouded Apollo butterflies from rivers (m).

found flying 10–150 m from rivers (92% of all sightings, Figure 6), usually within 10–50 m (73%).

However, due to the relatively low number of patches studied, the relation between abundance and habitat type (Paper III) was not statistically significant using single-factor dispersion analysis (p=0.226; Table 2). Similarly, the relations between abundance and area of patches, and abundance and perimeter of patches were not statistically significant; p=0.162 and p=0.980, respectively.

Table 2. Mean abundance of Clouded Apollos (standard deviation), area of patches (ha) and perimeter of patches (m) in different habitat types; *p*-value shows the level of statistical significance among the habitat types (dispersion analysis).

Habitat type	number	abundance (individuals)	area (ha)	perimeter (m)
dry meadow with strip of trees	11	155.5 (104.7)	1.95 (0.89)	743.0 (287.0)
dry meadow	2	110.0 (42.4)	1.52 (0.49)	783.9 (312.7)
wet meadow with strip of trees	3	250.0 (0.0)	2.97 (0.93)	740.2 (157.7)
p-value		0.226	0.162	0.980
Total	16	167.5 (96.64)	2.09 (0.93)	747.6 (254.85)

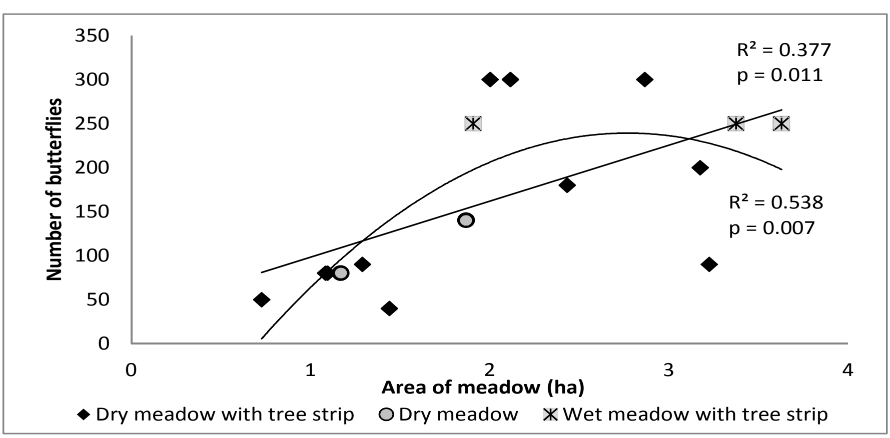


Figure 7. Regression analyses between abundance of Clouded Apollo and area of the patch (ha).

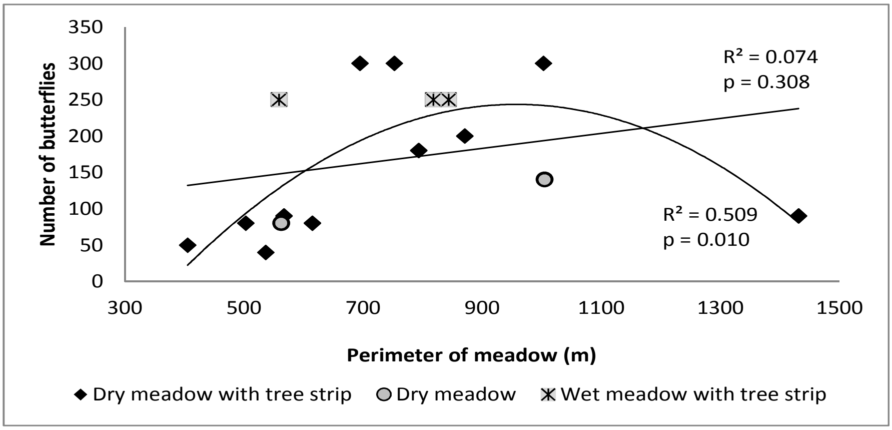


Figure 8. Regression analyses between abundance of Clouded Apollo and perimeter of the patch (m).

Linear regression models showed statistically significant relationships between butterfly abundance and size of meadow patch (R^2=0.377; p=0.011; Figure 7), but no significant relationship between abundance and perimeter of meadow patch (R^2=0.074; p=0.308; Figure 8). Quadratic regression models showed statistically significant relationships between the butterfly abundance and size of meadow patch (R^2=0.538; p=0.007) and butterfly abundance and perimeter of meadow patch (R^2=0.509; p=0.010).

5.3. Landscape factors influencing the Clouded Apollo and its distribution (Papers II and III)

In Southeast Estonia, the Clouded Apollo was found in 4 different locations close to the Estonian border from 1984 to 1986. These locations were situated 9–22 km apart, indicating immigration of the butterfly to Estonia from larger population in Russia. During subsequent years, the Piusa River subpopulation was established, with a large number of individuals moving relatively quickly into the new habitats. In 1990, the butterfly was found in the central Ahja River valley—40 km northwest of the line of first sightings (Figure 9). The butterfly formed a new subpopulation with large numbers of individuals that is still a strong subpopulation today.

In 1993, ten years after the first sightings in Southeast Estonia, the butterfly was found 75 km west of the line of first sightings, in the area of Puka. By the year 1995, the butterfly had formed a new subpopulation

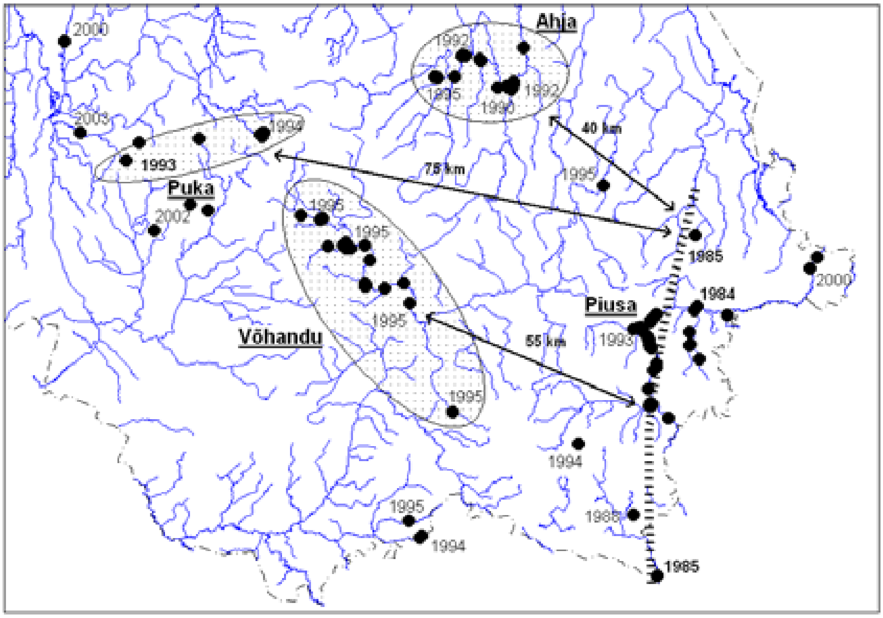


Figure 9. The distribution of the Clouded Apollo in South Estonia since 1984. Place names indicate name of subpopulation, years indicate year of sighting, horizontal bars indicate line of first sightings, and arrows indicate maximum distance from the line of first sightings.

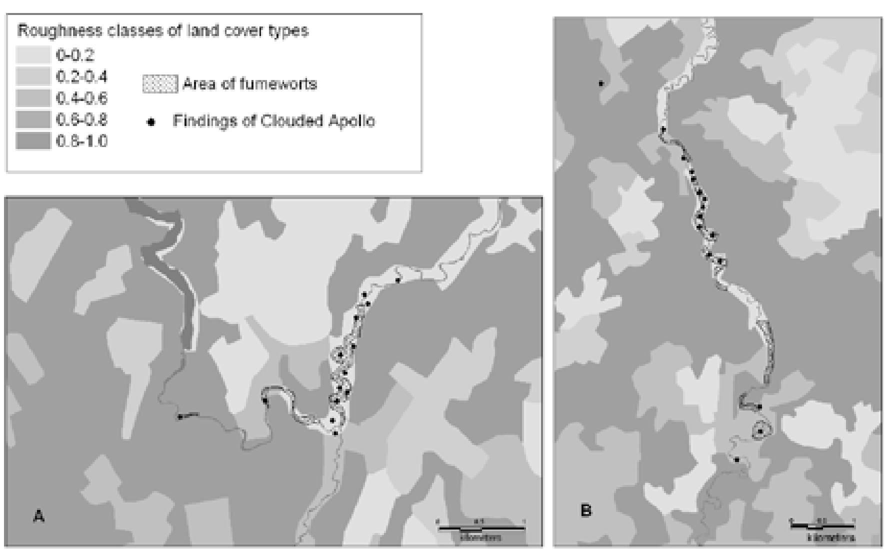


Figure 10. The openness of surrounding land cover types in the Ahja River (A) and Piusa River (B) valley subpopulations of the Clouded Apollo.

in the Võhandu River valley, situated up to 55 km west of the line of first sightings, and it remains a strong subpopulation today.

The analysis of surrounding land cover showed that the butterfly is found in narrow river corridors with riparian meadows, between tall forests (Figure 10). These meadows are close to rivers with narrow strips of trees; the primary tree species is grey alder (*Alnus incana*), the most common riparian tree in Estonia. Single trees of *Prunus padus*, *Fraxinus excelsior* and other deciduous trees and bushes are also found in these strips. The riparian alder strips are also the primary habitat of *Corydalis solida*—the food plant of Clouded Apollo larvae.

5.4. Socio-economic and land cover changes (Paper IV)

Since independence in 1991, tremendous structural changes have taken place in agriculture within Estonia. The re-orientation of agriculture to the new economic conditions has resulted in the marginalisation of rural areas. The relative share of agriculture in Estonia's GDP dropped from 19% in 1984, to 5.8% in 1997, and finally to 3.1% in 2002 (Estonian Rural … 2004). The unemployment rate has increased, and agricultural land has been set aside with nearly 25% of arable land in temporary disuse, and many people have moved away from rural areas. According to the SOA, out of 416 municipalities, the population dropped 10–40% in 83 rural municipalities, and 0–10% in another 80 municipalities during the 1990s. In 1960, 25.4% of all employed people were employed in agriculture; the percentage was 13.5% in 1980, 8.1% in 1996, and fell to 5.2% in 2000. Within just one decade, the number of people employed in agriculture decreased from 136,800 in 1990 to 31,500 in 2000. This decline lead to the disuse of large agricultural areas in semi-natural grasslands, and major land-use changes. However, substantial changes had already occurred after the Second World War. The area of forest has increased almost threefold from 1940 to 2000. This is primarily due to a large decrease in the area of natural grasslands, most of which are being overgrown by forests (Mander & Palang 1999). The highest level of agricultural production was at the end of the 1980s; subsequently, agricultural production has been decreasing steadily. For example, in the Puurmani community, the number of pigs decreased 24-fold during the period 1989 to 2001, the number of cattle decreased 1.6-fold, and the number of sheep decreased from 2145 before the war, to 6 in 2001. Numbers of all animals were even lower before the Second World War.

As a result, along the central portion of the River Pedja, out of 820 ha of former meadows and flooded meadows, 547.2 ha have become overgrown; 514 ha have been replaced by forests and 33.2 ha have been replaced by dense bushes between 1950 and 1990.

6. DISCUSSION

6.1. Distribution changes of the Clouded Apollo

The results of the study show that the Clouded Apollo is increasing in abundance and expanding its distribution in Estonia. Although the fragmented population of the island of Saaremaa has become extinct, in two other large populations—Northeast Estonia and South Estonia—the butterfly is numerous and is increasing its range. This differs from the general trends for most European grassland-specialist butterflies, and for the Clouded Apollo in other parts of its range, where it is in decline (Meglécz et al. 1999, Konvička & Kuras 1999, Välimäki & Itämies 2005, Franzén & Imby 2008, Aagaard et al. 2009). At the same time, there is also a decline in extensive agriculture in Estonia, and many semi-natural grasslands are abundant. However, it appears that there is still suitable habitat for the Clouded Apollo, particularly in South Estonia, where the butterfly has expanded very rapidly to occupy a large area; in Northeast Estonia this expansion has been slower. The Clouded Apollo is usually considered a sedentary species (Välimäki & Itämies 2003), but in our study, the butterfly moved a straight-line distance of up to 75 km over 10 years, and 40 km over 6 years, or approximately 6.5 to 7.5 km a year. It can be argued that the assessment of movement is based on sightings and not on mark-release-recapture (MRR) data. Dates of sightings can vary significantly from the timing of the actual movements, but they are probably reliable because the areas were visited frequently by entomologists, particularly in the regions of Piusa and Puka, and this butterfly always receives ample attention. In reality, the butterfly does not disperse in a linear fashion. It is possible that the Clouded Apollo first moved to the Võhandu area and from there to Puka because the Võhandu valley was only location poorly studied during these years; this makes the possible route of butterfly movement many kilometres longer. The rapid range expansion of the Clouded Apollo is also supported by the observation that, 21 years later in 2005, the butterfly was found near Kilingi-Nõmme, 145 km west of the location of first sightings in Southeast Estonia.

The MRR studies of Clouded Apollos (Konvička & Kuras 1999, Meglécz et al. 1999, Välimäki & Itämies 2003, Gorbach & Kabanen 2010) have all shown that the Clouded Apollo butterfly moves rather short distances. For example, Gorbach & Kabanen (2010) found that the average movement distance of the Clouded Apollo was 120 m and the maximum distance 2.68 km; Välimäki & Itämies (2003) found similar values of 142 m and 1.35 km, and Konvička & Kuras (1999) calculated values of 232 m and 2.55 km, respectively. A similar study conducted in Estonia by Anu Sang (2007) also found that the mean movement distance of the Clouded Apollo was 143 m and the maximum distance 884.6 m. However, the MRR method can underestimate the movement of a species. One important factor is the size of the dispersal study area. For example, Franzén and Nilsson (2007) found that realistic estimates of dispersal distance require a study area of at least 50 km^2, which is not typically covered by the MRR method. Therefore, it is possible that under suitable conditions, the Clouded Apollo can move much longer distances; this is supported by our simple study of appearances and sightings that precisely describes the distribution of the species over time, and encompasses a larger area than a MRR study.

6.2. Habitat preferences of the Clouded Apollo

The distribution data showed that the Clouded Apollo has moved relatively rapidly into large areas, which can be explained by the availability of high quality habitats. Habitat quality can be defined as the sum of environmental conditions necessary for individual and population persistence (Hall et al. 1997).

One of the primary factors influencing the habitat quality of habitat for butterflies is the presence of nectar-rich flowers. This has been confirmed for the Clouded Apollo (Luoto et al. 2001), and in our study the butterfly was primarily found in the species-rich semi-natural meadows that are the best nectar sources in Estonia. Another important factor is sites for mating and breeding, for which the Clouded Apollo needs open meadows (Välimäki & Itämies 2003, Bergström 2005). Our study confirmed that the butterfly was found primarily in open semi-natural meadows. Several butterflies benefit from the forest edges that provide several favourable conditions (Liivamägi et al. 2014). Being large and a poor flyer, the Clouded Apollo requires shelter, and therefore often flies close to forest edges; they fly particularly close to shorter deciduous forests and bushes, whereas taller sharp forest edges can constitute a barrier for the butterfly (Konvička et al. 2007). Although in our study, most of sightings of the butterfly were close to the riparian strips with deciduous trees and bushes, in 73% of cases the butterfly flew a distance of 10–50 m from the water body with the riparian strip. However, the shelter may not be the only reason the butterfly is flying close to the riparian strip. As a monophagous butterfly, the Clouded Apollo is also dependent on the food plant of the larvae (Konvička & Kuras 1999, Luoto et al. 2001, Bergström 2005). In Estonia, the larvae feed on *C. solida*, which grows on the banks of the rivers under a relatively narrow strip of trees, primarily alders. Therefore, the butterfly should prefer habitats that are also the habitat of the larval food plant. It is possible that the Clouded Apollo is keeping close to the deciduous trees and bushes as they track the habitat features associated with the larval food plant during egg laying because the food plant itself is neither flowering nor growing (Konvička et al. 2007). Based on our data and observations, this could be the primary reason why the butterfly remains close to the riparian strips. Most of the habitats of the butterfly coincided with the distribution of *C. solida*, both on the national scale and on the scale of individual habitats. The most frequent habitat type (69%) for the Clouded Apollo was dry semi-natural meadows with a riparian strip of alders and bushes, which was also the habitat of *C. solida*, and the butterfly was primarily found close to the alder strips. The importance of deciduous forests for the Clouded Apollo has also been stressed by other authors (Luoto et al. 2001, Välimäki & Itämies 2003, Heikkinen et al. 2007, Gorbach & Kabanen 2010).

The analysis of openness in the surrounding landscape of the Ahja River and Piusa River subpopulations showed that the butterfly was found in a narrow corridor of meadows surrounded by tall forests, primarily pine forests. In the centre of the corridor was the river with the strip of alders, where most of the *C. solida* and the butterflies were found. Although there were other nectar-rich meadows in the area, neither the butterflies nor *C. solida* was found in these biotopes.

Another important condition is a suitable size of habitat for different species. In general, the abundance of butterflies increases with the size of habitat patches (Krauss et al. 2003, Öckinger et al. 2012). However, different species may require different patch sizes, particularly specialist species (Dover & Settele 2009, Rosin et al. 2012). In our study, the meadows on the riverbanks were relatively small. The largest number of Clouded Apollo individuals was found in habitats with of 1–3 ha. It can be assumed that this is the optimal habitat size for this butterfly. This preference for smaller habitats can be explained because as habitats become larger they become more open, and the Clouded Apollo prefers forest edges and strips as the habitat for the larval food plant and for movement and shelter.

These factors influencing habitat quality may be the reasons why the butterfly has expanded its distribution relatively rapidly, and established new subpopulations with significant numbers of individuals in Estonia.

6.3. Landscape factors influencing the Clouded Apollo and its distribution

The increase in the abundance and distribution of the Clouded Apollo is also probably supported by presence of suitable landscape structure within Estonia. The studies in the central Ahja River and Piusa River valleys showed that the Clouded Apollo prefers relatively small semi-natural grassland patches on the banks of rivers surrounded by forests or strips of trees. Such habitats are typically isolated, resulting in fragmentation of populations. In Estonia, most of the sightings of the Clouded Apollo are from the river valleys, and the distribution of inhabited patches follows the river system, keeping patches close together and forming a continuum between habitat patches. One reason for the rapid movement of the Clouded Apollo in South Estonia, in addition to the existence of high quality habitat, may be the landscape structure provided by rivers that connects suitable habitats, creating a corridor system with stepping stones composed of high quality habitats. Rivers provide semi-natural meadows on their floodplains, riparian trees for larval food plants, shelter for the imago and open corridors enabling butterflies to fly through the tall forest areas. The Clouded Apollo is also found in other northern countries close to rivers and river valleys (Luoto et al. 2001, Bolotov et al. 2013), which may be a feature of the northern population.

6.4. Socio-economic and land cover changes

During the last century, several political events have led to significant socio-economic changes in Estonia. Because of these changes, there have been large shifts in land use and agricultural practises (Mander & Palang 1999, Estonian Rural… 2004, Kukk & Sammul 2006). The primary result has been overgrowth of small isolated meadows that were cultivated by traditional extensive agricultural practices such as mowing by hand, or grazing by cows and sheep. As a result, there has been a drastic decrease in the area of ecologically valuable habitats related to extensive agriculture, such as wooded meadows and coastal meadows (Kaasik et al. 2011). As observed from the example of the Puurmani community, similar trends have been observed in the flooded meadows of rivers that are primary habitat of the Clouded Apollo, where the butterfly was found in 2010. In the Puurmani community, a substantial decrease in human and animal populations has taken place, particularly during last 20 years. The most drastic decrease was in the number of sheep, related to traditional agriculture. An additional reason for large changes in this area was that between 1952 and 1991, the area belonged to the Red Army and was entirely closed to the public. As a result, many people moved away from the area, farms were set aside, and only ruins remain of the former farmsteads. Almost 70% of the floodplains and wooded meadows of the River Pedja became overgrown during the Soviet period, from 1950 to 1990. These historic changes indicate that even if we have suitable and high quality habitat for the Clouded Apollo now, these habitats are very vulnerable and can overgrow during a relatively short period, resulting in the loss of habitat for the Clouded Apollo. During recent years, the environmental support for management of flooded meadows has kept some of the meadows open. At the same time, they are still in danger of abandonment because small semi-natural meadows are not a high priority for farmers and can overgrow very quickly. A management strategy for species protection must pay special attention to keeping extensive agricultural practices operating in the habitats of protected species, including the Clouded Apollo, to avoid loss of their habitats.

7. CONCLUSIONS

The results of the thesis show that the abundance and range of the Clouded Apollo have increased in recent years in Estonia, which is the opposite trend from that observed in the rest of Europe. The reason for this increase appears to be the availability of high quality habitats with ideal landscape structure for the butterfly. The preferred habitats of the Clouded Apollo were semi-natural meadows with strips of alders, located on the banks of rivers. Rivers create natural corridors between isolated patches of metapopulations, and may have made an important contribution to the current distribution of the butterfly. The Clouded Apollo is a species that clearly benefits from corridors in the landscape that increase the butterfly's mobility. However, these semi-natural meadows are very vulnerable to overgrowth. Vigilance is needed to avoid the overgrowth of these meadows and to ensure the necessary density of suitable habitats that creates corridors and stepping stones for the distribution of the species.

The main conclusions of the thesis are:

- The abundance and range of the Clouded Apollo have increased during recent decades in Estonia.
  - Since 1984, a new population of Clouded Apollo has become established in South Estonia that has increased in abundance and expanded its distribution. The Saaremaa population has become extinct; the last sighting of the Clouded Apollo was in 1973.

- The preferred habitat of the Clouded Apollo is semi-natural meadows with a strip of alders located on the banks of rivers.
  - Riparian meadows with alder strips possess proper conditions for the primary requirements of the Clouded Apollo: nectar sources for the imago, sites for mating and breeding, shelter for the imago, and food plants for the larvae.
  - The distribution of the Clouded Apollo coincides with the distribution of the larval food plant, *Corydalis solida*.

- Landscape structure plays an important role in the distribution of the Clouded Apollo.
  - Rivers create a natural ecological network for the dispersal of the Clouded Apollo, providing suitable habitats, migration corridors, and stepping stones through biotopes that are barriers for the butterfly.

- High quality habitats and proper landscape structure may facilitate rapid migration of the Clouded Apollo, which approached 6.5 to 7.5 km a year in the South Estonia population.
  - The combination of semi-natural meadows as nectar sources and mating places for the imago, rivers as open movement corridors, and riparian strips as areas of shelter and habitat for the food plant of monophagous larvae, constitutes high quality habitat for the Clouded Apollo.

- Political and socio-economic changes have led to large shifts in agricultural practises and land use during the last century.

- Semi-natural meadows are one of the most vulnerable biotopes in Estonia. As the primary habitat for the Clouded Apollo, attention is needed to avoid a decrease in these valuable habitats.

- The management of the Clouded Apollo should consider the preservation of high quality habitats and their proper density and connectivity in the landscape to ensure preservation and continued dispersal of this protected butterfly.

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SUMMARY IN ESTONIAN

Mustlaik-apollo [*Parnassius mnemosyne* (L.)] levik ja elupaiga eelistused Eestis

Euroopa liblikate punase nimestiku andmetel on 31% Euroopa liblikaliikide arvukus kahanemas ning ligikaudu 9% liikidest on ohustatud. Rohumaa spetsialisti mustlaik-apollo (*Parnassius mnemosyne*) levik ja arvukus on kogu Euroopas vähenenud. Selle peamisteks põhjusteks on elupaikade killustumine ja kadumine maakasutuse muutuste tagajärjel, traditsioonilise põllumajanduse vähenemine ning karjatamise ja niitmise lõpetamine poollooduslikel niitudel.

Eestis, erinevalt teistest Euroopa riikidest, on mustlaik-apollo arvukus ja levikuala viimaste kümnendite jooksul suurenenud. See annab põhjust uurida täpsemalt mustlaik-apollo levikut ning selle seoseid tema elupaiga ning ümbritseva maastiku struktuuriga.

Mustlaik-apollo on ratsulibliklaste sugukonda kuuluv suur valge liblikas, kelle röövik on monofaag, toitudes ainult perekond *Corydalise* (lõokannuse) liikidel. Vastavalt Rahvusvahelise Looduskaitseliidu IUCN punase nimestiku kriteeriumitele kuulub mustlaik-apollo liikide gruppi, mille esinemis- ja levikuala ning elupaiga kvaliteet vähenevad. Seetõttu on liik kaitstud Berni leppe ja Euroopa Liidu loodusdirektiiviga Natura 2000 ning lisatud Euroopa liblikate punasesse nimestikku. Eestis on mustlaik-apollo seadusega kaitstud alates 1995. aastast ja kuulub II kaitsekategooria liikide hulka.

Eestis on mustlaik-apollol kolm isoleeritud populatsiooni ning vastavalt sellele on eristatud ka 3 alamliiki: *P. mnemosyne osiliensis* (Bryk 1922) Saaremaal; *P. mnemosyne estonicus* (Viidalepp 2000) Põhja-Eestis ja *P. mnemosyne viidaleppi* Lõuna-Eestis (Kesküla & Luig 1997). Saaremaa populatsioon on tõenäoliselt välja surnud, kuna viimane leid on sealt aastast 1973. Põhja- ja Lõuna-Eesti populatsioonides on mustlaik-apollo oma arvukust ja levikuala suurendanud.

Antud doktoritöö eesmärkideks oli:

- uurida mustlaik-apollo arvukuse ja leviku muutusi Eestis kogu perioodi jooksul, mille kohta on võimalik leiuandmeid saada;
- selgitada välja mustlaik-apollo elupaigaeelistused Eestis;

- analüüsida maastiku mõju mustlaik-apollo levikule;
- uurida sotsiaal-majanduslike ja maakasutuse muutuste mõju poollooduslikele kooslustele Eestis viimase 50 aasta jooksul.

Doktoritöö tulemusena selgus, et mustlaik-apollo arvukus ja levik Eestis suureneb. Isegi kui Saaremaa populatsioon on välja surnud, on Põhja- ja Lõuna-Eesti populatsioonides suurel arvul liblikaid ja need populatsioonid laienevad jõudsalt. Ligikaudu 2/3 viimaste aastakümnete mustlaik-apollo leidudest tuleb Lõuna-Eesti populatsioonist. Saadud tulemus on küllaltki erinev üldisest suundumusest Euroopas, kus mustlaik-apollo arvukus pidevalt väheneb.

Siiani on mustlaik-apollot peetud väheliikuvaks või paikseks liigiks. Märgistus-taaspüügi (MRR-) meetodil läbi viidud uuringud näitavad, et ta läbib küllaltki lühikesi vahemaid. Käesolevas doktoritöös põhineb liigi levikumuutuste hindamine liblika leiuandmetel ning liigi levikut kirjeldatakse suuremal alal pikema aja jooksul. Leviku uuringute tulemusena selgus, et Lõuna-Eesti populatsioonis on mustlaik-apollo liikunud kümne aasta jooksul edasi kuni 75 km, mis teeb ligikaudu 7 km aastas. Seetõttu on võimalik, et sobivate tingimuste olemasolul võib mustlaik-apollo läbida palju suuremaid vahemaid ja levida palju kaugemale kui on varem arvatud.

Üks võimalik põhjus mustlaik-apollo kiirele levikule Lõuna-Eestis on sobilik maastikustruktuur. Suurem osa Eesti mustlaik-apollo leidudest on jõgede orgudest ja liblika levik ning asustatud elupaigalaigud järgivad jõgede süsteemi. Jõed moodustavad loodusliku rohevõrgustiku ehk suure ühenduskoridoride süsteemi koos astmelaudade ja tuumalade ehk kõrge väärtusega elupaikadega. Jõed ühendavad eraldi asuvaid mustlaik-apollole sobilikke elupaiku, mis võimaldab liblikatel lennata läbi metsaalade, mis muidu oleksid takistaksid nende levikut. Samuti esinevad jõgede ääres mustlaik-apollole elupaigaks sobilikud poollooduslikud niidud ja puuderibad koos rööviku toidutaime hariliku lõokannusega (*Corydalis solida)*.

Mustlaik-apollo küllaltki kiiret levikut uutele aladele toetab ka sobivate elupaikade olemasolu. Üks peamistest teguritest, mis mõjutab liblikate elupaiga väärtust, on nektaritaimede ohtrus ja liigirikkus. Teine oluline tegur on paaritumis- ja sigimiskohtade olemasolu, seetõttu vajab mustlaik-apollo avatud niitusid. Kolmandaks sõltub rohumaa spetsialist mustlaik-apollo rööviku toidutaime olemasolust. Eestis toitub mustlaik-apollo röövik harilikul lõokannusel, mis kasvab jõgede kallastel puude, peamiselt leppade läheduses. Seega tagavad jõgedeäärsed puuderibad rööviku toidutaimedele ideaalse kasvukoha. Suurte liblikate jaoks on väga oluline tuulevarju olemasolu. Mustlaik-apollo lendab tihti metsa servas ja põõsastikes ning hoiab jõgedeäärsete puuderibade lähedusse. Seetõttu on servaalade olemasolu mustlaik-apollole oluline, samas võivad kõrged okaspuud tema levikut takistada. Liblikate jaoks on oluline ka sobiva elupaiga suurus. Kõige rohkem leiti mustlaik-apollo isendeid jõgedeäärsetelt niitudelt pindalaga 1–3 ha, mis võiks olla talle sobivaim elupaigalaigu suurus. Tõenäoliselt on suuremad elupaigad liblika jaoks liiga avatud. Elupaiga uuringud Ahja ja Piusa jõe keskosas näitasid, et mustlaik-apollo eelistab väikesi poollooduslikke kuivi niite jõgede kallastel, mis on ümbritsetud metsa või puuderibaga.

Ümbritseva ala maakatte tüübi analüüs näitas, et mustlaik-apollo eelistab kitsaid jõekoridore jõgedeäärsete niitudega, mida ümbritsevad kõrged okaspuumetsad. Nendel niitudel on vahetult jõe ääres ka kitsas puuderiba, kus on peamiseks puuliigiks hall lepp (*Alnus incana*), mis on kõige tavalisem jõgede ääres kasvav puuliik Eestis. Jõgedeäärne leppadega kaldariba on ka peamine hariliku lõokannuse kasvukoht. Mustlaik-apollo ja tema rööviku toidutaime hariliku lõokannuse levikumuster on omavahel kooskõlas.

Levikuks soodsate tingimuste, sobiliku maastikustruktuuri ja kõrge väärtusega elupaikade olemasolu võiks olla põhjuseks, miks Eestis on mustlaik-apollo viimastel kümnenditel suhteliselt kiiresti levinud ja oma arvukust suurendanud.

Poollooduslikud niidud, mis on mustlaik-apollo peamiseks elupaigaks ja hariliku lõokannuse peamiseks kasvukohaks, on seotud traditsioonilise põllumajandusega. Eestis, nagu ka mujal Euroopas, väheneb traditsioonilise põllumajanduse osakaal ja paljud poollooduslikud niidud on maha jäetud. Poollooduslike niitude pindala on vähenenud 1 571 000 hektarilt 1939. aastal kuni 130 000 hektarini 2006. aastal. Pedja jõe lammialal on alates 1950-ndatest kinni kasvanud 547 ha endisi niite ja lamme, 514 ha on asendunud metsaga ja 33 ha kattunud tiheda põõsastikuga. Samas on Eestis praegu veel praegu mustlaik-apollole sobivaid elupaiku, kuid need võivad hooldamata jätmise korral väga kiiresti kinni kasvada. Poollooduslike niitude viimaste aastate hooldamistoetused on siiski hoidnud paljusid niite avatuna.

Antud doktoritöö tulemused näitavad, et mustlaik-apollo arvukus ja levik on Eestis viimastel aastatel suurenenud, mis on vastupidine suundumus ülejäänud Euroopas toimuvale. Selle põhjuseks on kõrge väärtusega elupaikade ja liblika jaoks ideaalse maastikustruktuuri jätkuv olemasolu. Mustlaik-apollo eelistatumad elupaigad on poollooduslikud niidud, mis asuvad jõgede kallastel ja mille ääres on puuderiba, enamasti lepariba. Jõed moodustavad looduslikke koridore ehk ühendusi üksteisest eraldatud elupaigalaikude vahel ja võivad oluliselt soodustada liblika levikut. Samas on mustlaik-apollole elupaigaks sobivad poollooduslikud niidud väga tundlikud hooldamata jätmise suhtes. Selliste niitude kinnikasvamist tuleks igati vältida, et tagada vajalik mustlaik-apollole sobilike elupaigalaikude tihedus, astmelauad ning koridorid haruldase kaitsealuse liblikaliigi säilimiseks ja levimiseks.

Doktoritöö peamised järeldused:

- Mustlaik-apollo arvukus ja levikuala on Eestis viimaste kümnendite jooksul suurenenud.
    - Alates 1984. aastast on Lõuna-Eestis uus mustlaik-apollo populatsioon, mis on suurendamas oma arvukust ja levikut. Saaremaa populatsioon on välja surnud.

- Mustlaik-apollo eelistatuimaks elupaigaks on väikesed poollooduslikud niidud jõgede kallastel koos puuderiba, enamasti leppadega.
    - Jõgedeäärsed leparibaga poollooduslikud niidud moodustavad kõrge väärtusega elupaiga, kuna vastavad kõikidele peamistele mustlaik-apollo elupaiga nõudlustele: on olemas nektarivarud, avatud paaritumis- ja sigimispaigad, monofaagist rööviku toidutaime lõokannuse kasvukohad, jõgedeäärsed puuderibad kui tuulevari ja varjumiskoht ning jõed kui avatud liikumis- ja levikukoridorid.
    - Mustlaik-apollo levikualad on vastavuses rööviku toidutaime, hariliku lõokannuse kasvukohtadega.

- Maastiku struktuur mängib olulist rolli mustlaik-apollo levikus. Jõed moodustavad loodusliku rohevõrgustiku, tagades liblikale levikuks sobilikud elupaigad, levikukoridorid ja astmelauad läbi nende biotoopide, mis on talle levikubarjääriks.
    - Kõrge kvaliteediga elupaigad ja sobiv maastikustruktuur toetavad mustlaik-apollo kiiret levikut Eestis, mis on jõudnud Lõuna-Eesti populatsioonis ligemale 7,5 kilomeetrini aastas.

- Viimase sajandi jooksul toimunud poliitilised ja sotsiaal-majanduslikud muutused on viinud suurte muutusteni Eesti põllumajanduses ja maakasutuses.

- Eestis on ühed kõige haavatavamad biotoobid poollooduslikud kooslused. Olles mustlaik-apollo peamisteks elupaikadeks, tuleb vältida nende väärtuslike elupaiga tüüpide vähenemist ja kadumist.

- Mustlaik-apollo kaitseks peab säilitama sobiva tihedusega omavahel seotud kõrge kvaliteediga elupaigad, et tagada ka elujõuliste liblikapopulatsioonide säilimine ja levik.

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I

ORIGINAL PUBLICATIONS

Liivamägi, A., Kuusemets, V., Luig, J. & **Kask, K.** 2013.

CHANGES IN THE DISTRIBUTION OF CLOUDED APOLLO *PARNASSIUS MNEMOSYNE* (*LEPIDOPTERA: PAPILIONIDAE*) IN ESTONIA.

Entomologica Fennica 24 (3): 186–192.

Changes in the distribution of Clouded Apollo *Parnassius mnemosyne* (Lepidoptera: Papilionidae) in Estonia

Ave Liivamägi, Valdo Kuusemets, Jaan Luig & Kadri Kask

Liivamägi, A., Kuusemets, V., Luig, J. & Kask, K. 2013: Changes in the distribution of Clouded Apollo *Parnassius mnemosyne* (Lepidoptera: Papilionidae) in Estonia. — Entomol. Fennica 24: 186–192.

Clouded Apollo (*Parnassius mnemosyne*) has been occupying three separate areas in Estonia and has increased its abundance and population area remarkably during the last 30 years. Since the butterfly was first identified in the northeast (1878) and southeast (1984) of Estonia, the species has expanded its distribution with overall expansion distances of approximately 135 and 100 km, respectively. In western Estonia, the butterfly was found locally on the island of Saaremaa in 1922–1973. Today, the butterfly is most likely extinct there. The occupational trend of the species in Estonia is not in accordance with its general trend in Europe, where it has shown a continuous decline. We suggest that in Estonia there is a suitable landscape structure with the presence of suitable landscape elements and still enough semi-natural grasslands that are suitable habitats for the butterfly even despite the fact that the traditional extensive agricultural practice in general is decreasing in Estonia.

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1. Introduction

Many European butterfly species are endangered, and their distribution has declined during recent decades (Van Swaay *et al.* 2010). One widely distributed and endangered specialist species that has received much attention over recent decades and that has been well studied by several researchers (Konvička & Kuras 1999, Meglécz *et al.* 1999, Luoto *et al.* 2001, Välimäki & Itämies 2003, Meier *et al.* 2005, Gratton *et al.* 2008, Gorbach & Kabanen 2010) is Clouded Apollo, *Parnassius mnemosyne* (Linnaeus 1758). Over the entire distribution range, this Palaearctic species has discrete populations. In Northern Europe, the species occurs in flat semi-natural grasslands (Luoto *et al.* 2001, Meier *et al.* 2005), but in Central Europe, it is found in forest steppes, sparse deciduous forests and forest clearings (Konvička & Kuras 1999).

The distribution and abundance of Clouded Apollo has declined in North Europe, e.g. Finland (Väisänen & Somerma 1985), Sweden (Bergström 2005), Norway (Aagaard & Hansen 1992), and in Central Europe (Konvička & Kuras 1999). However, there are few studies providing evidence in which *P. mnemosyne* has increased its abundance and expanded its distribution area (see Gorbach & Kabanen 2010).

Due to the vulnerability of the populations of Clouded Apollo and due to several reports about local extinctions or the limited distribution of populations (Bergström 2005), the species is protected in Europe by the Bern Convention, the EU Habitat Directive Natura 2000 (CEE Habitat Directive 43/92, annex IV), and national protection acts, and it is included in many regional Red Data Books. In Estonia, the butterfly has been under legal protection since 1995.

Clouded Apollo has been occupying three geographically separate areas in Estonia: west, northeast and southeast. In accordance with a regional separation, three subspecies have been described: *P. mnemosyne osiliensis* (Bryk 1922) in Saaremaa Island; *P. mnemosyne estonicus* (Viidalepp 2000) in north-eastern Estonia, and *P. mnemosyne viidaleppi* (Kesküla & Luig 1997) in south-eastern Estonia. The first record of *P. mnemosyne* in north-eastern Estonia was in 1878. In 1922 the butterfly was discovered on the island of Saaremaa and in 1984 in southern part of Estonia. The last information of the existence of the species on the island of Saaremaa is from 1973. During the same year, 2 individuals were caught and 30 were reported to be seen (Kesküla 1989). There are no later records from the area, despite that many entomologists have searched for the butterfly. The subspecies is probably extinct today. In two other parts of Estonia, Clouded Apollo has expanded its distribution.

The geographical distribution of Clouded Apollo is generally related to the distribution of its host plants and to certain environmental conditions required by the given species. The larva of the species is monophagous on the plant genus *Corydalis*. In Estonia, they mainly feed on the leaves of *C. solida*. Therefore, the distribution of Clouded Apollo depends on the distribution of its larval host plant species.

The other general factors that make a biotope suitable for Clouded Apollo are food resources for adults, suitable habitat patches and surrounding landscape structure. Due to the specific requirements of environmental and habitat conditions, populations of Clouded Apollo are in danger of becoming fragmented, which may lead to the extinction of the butterfly. Therefore, it is important to study the state and distribution changes of Clouded Apollo in different parts of its distribution.

The aim of this study was to examine the abundance and distribution changes of Clouded Apollo in Estonia during the period of 1878–2010. Understanding the pattern of the distribution and abundance of the butterfly is necessary for planning effective conservation of the species.

2. Material and methods

We collected and organised all known records of the findings of Clouded Apollo in Estonia to a database. The database includes data from various sources, such as literature, insect collections, records from researchers and local surveys of the butterfly. Whereas the purpose of the studies and the collections of the butterfly have differed and have been performed by different groups of people (amateur lepidopterists, qualified lepidopterists, volunteers), there are several duplications of records and variation in the accuracy of data.

Most of the earlier records were more general, describing the name of the place or the description of the location using landmark features such as roads, rivers, trees and bushes, some of the data were described within a 10 x10 km UTM square. The accuracy of these data was several kilometres but at least 5 km.

The records from years 1981–2010 were taken from the national periodical review called LepInfo (a publication of the Estonian Lepidopterologists' Society and the Section for entomology of the Estonian Naturalists' Society that collects all findings of most butterfly species in Estonia). The accuracy of these records is generally better than in the case of older data, because all records are fixed according to the coordinates of the Estonian national grid system (10 × 10 km) and concurrently international UTM grid system. During the last ten years, records of the butterfly (and the exact position of the habitat patch) have been additionally collected by the authors of this paper using portable GPS units.

The accuracy differs among separate data sets but in all it is adequate for analysing the species distribution for the scale of the whole Estonian during the long time period (132 years) since the first record of Clouded Apollo in Estonia.

All descriptions of the findings of the butterfly were linked on a digital cadastral map of Estonia (1:10,000) to the common GIS database using MapInfo Professional 9.0. The database of

Table 1. Summary of records of *Parnassius mnemosyne* in Estonia.

Study periods	Regions	No. of findings per region	No. of sites per region	No. of individuals per site
	NE	32	8	1–44
1878–1969	W	9	1	1–20
	SE	–	–	–
	NE	12	6	1–17
1970–1979	W	1	1	–
	SE	–	–	–
	NE	19	11	1–37
1980–1989	W	–	–	–
	SE	13	9	1–9
	NE	14	11	1–50
1990–1999	W	–	–	–
	SE	81	42	1–200
	NE	57	48	1–60
2000–2010	W	–	–	–
	SE	69	44	1–300

Clouded Apollo consists of data about the exact location of the findings (place name or coordinates if possible), class of accuracy on a 1–3 scale (1: exact location, 2: grid system coordinates, 3: descriptive location), date and time of the observation, name of the observer, gender and the number of individuals if determined and counted, source of data and a short description of the habitat. For analyses of the distribution changes we divided our data into five study periods: 1878–1969, 1970–1979, 1980–1989, 1990–1999 and 2000–2010. The first period is longer than the rest, because there were only single records of the butterfly from this period.

Finally, for the general evaluation of the relations between the distribution of the butterfly and its larval food plant *Corydalis solida*, the distribution map of the plant species in Estonia was derived from the Atlas of the Estonian Flora where the data are displayed in a grid of 9 × 11 km squares (Kukk & Kull 2005).

3. Results

There are 307 records of Clouded Apollo in Estonia from the period 1878–2010. Of the five study periods, most records of distribution (82%) are from 1980 and later. Only 18% of all records are from the period 1878–1979.

During the first study period 1878–1969, there are 41 records of Clouded Apollo, with the majority of them located in eight places in north-eastern Estonia and only one location (Kübassaare) on the island of Saaremaa (Table 1). During the period 1970–1979, there are 13 records with the majority of them located in north-eastern Estonia and one on the island of Saaremaa. During these two study periods the number of individuals of *P. mnemosyne* seen at the sites of findings varied between 1–44. During the period 1980–1989, there are 32 records in Estonia. The butterfly was registered 19 times in north-eastern and 13 times in south-eastern Estonia. Number of individuals varied between 1 and 37. During the period 1990–1999 and 2000–2010, there are 95 and 126 records of *P. mnemosyne*, respectively. Approximately two thirds of the findings from the last two study periods are locating in south-eastern Estonia where the number of recorded individuals has reached 300.

Changes in the distribution trends of Clouded Apollo in Estonia are shown in Fig. 1. During the period 1878–1969, the distribution of the butter-

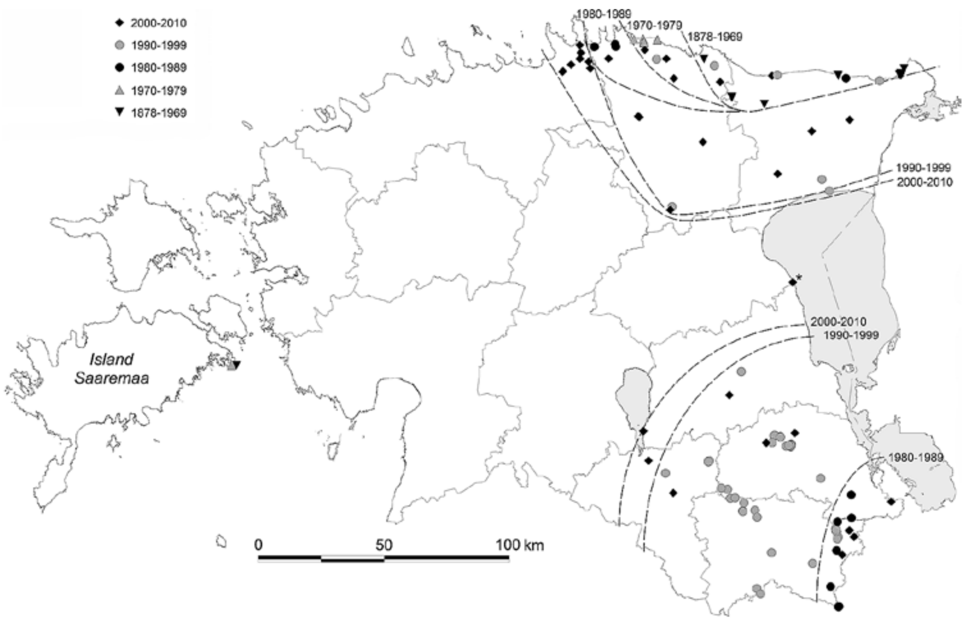

Fig. 1. Distribution of Clouded Apollo (*Parnassius mnemosyne*) in Estonia in 1878–2010. Broken lines show the extent of the butterfly distribution in a given period. The record with an asterisk (*) concerns a single instance from the year 2002 (5 individuals) with no records there later. Therefore, the 2000–2010 line was not drawn to include this record.

fly remained local in north-eastern Estonia. During the periods 1970–1979 and 1980–1989, the species moved westward, with decennial maximum expansion distances of approximately 30 km and 20 km, respectively (Fig. 1). During the last two decades (1990–1999, 2000–2010) the expansion of the butterfly has continued to the west and to the south. In contrast, on the island of Saaremaa the butterfly was found during the period 1922–1973 but it remained local and few in numbers in its habitats over the entire period.

Until the middle of the 1980s, Clouded Apollo was found only in north-eastern Estonia and on the island of Saaremaa. In southern Estonia the butterfly was first recorded in 1984 near to the rivers Pedetsi and Piusa. Six years later, the butterfly was already found approximately 40 kilometres to the north in the Ahja River catchment and five years later approximately 35 kilometres to the northwest in the Võhandu River catchment. A more substantial increase, 30 to 50 km in occupancy to the north and north-westerly directions, was observed in the period 1990–2000.

The distribution pattern of Clouded Apollo in Estonia and that of its larval host plant *Corydalis solida* are generally consistent (Figs 1 and 2). *Corydalis solida* is mainly growing in northern and south-eastern part of Estonia and in some areas on islands. The plant is almost missing in the central part of Estonia. Only in north-western part there are areas with *C. solida* but no findings of Clouded Apollo.

4. Discussion

The data sets used in our study differed in quality, but we consider their precision adequate for analysing the distributional changes of *P. mnemosyne* in the scale of whole Estonia during the long time period. However, one can suspect more representative recording effort in the recent data than in the older ones. We concur that recent recording tends to be more systematic and organised. On the other hand, entomologists had been visiting similar habitats suitable for *P. mnemosyne* also in earlier years, and a rare butterfly species has re-

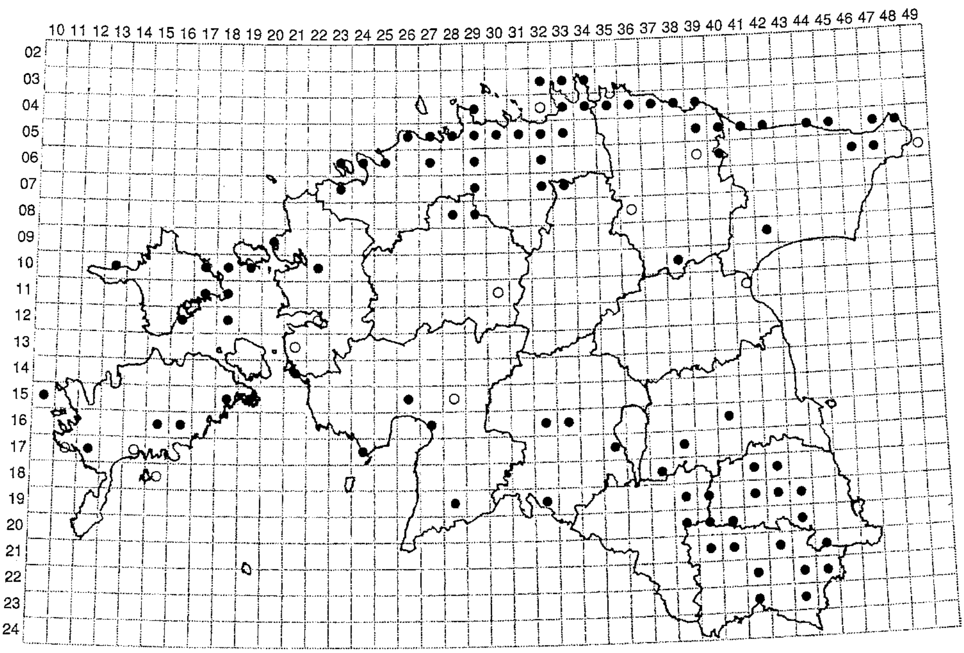

Fig. 2. The distribution of *Corydalis solida* in Estonia in 1921–2005 is displayed in a grid of 9 × 11 km squares. Empty circle: recorded in 1921–1970; filled circle: recorded in 1971–2005 (Kukk & Kull 2005).

ceived a lot of attention through the decades and is often recorded more carefully than common species. Therefore, we expect that presence of Clouded Apollo in certain areas would have been noticed whereas unrepresentative recording of *P. mnemosyne* especially in different locations is not the issue of this study. Additionally, there is no reason to doubt the study effort in the three regions of Estonia where the species is present. Since the area of the country is relatively small, practically the same amount of attention has been paid to butterfly research all over Estonia. It should be noted that the number of the lepidopterists has been almost the same through the times.

The general distribution pattern of Clouded Apollo in Estonia is in good agreement with the distribution of its larval host plant species. Interestingly, *C. solida* has not been recorded in central Estonia and most probably because of that the butterfly has neither been recorded there. Furthermore, this phenomenon offers a plausible explanation why the butterfly occupies three geographically separated areas in Estonia. Since there are rather long distances between these three regions and because the initial findings of the butterfly in the regions came from different years, we suggest that the colonisation of these three regions by Clouded Apollo took place from different directions. For instance, to North Estonia the butterfly probably expanded from Russia, to south-eastern Estonia from North-East Latvia or Russia (Pskov region) and to Saaremaa from western Latvia. This is supported by the general distribution areas of Clouded Apollo in neighbouring countries. However, there is no certain evidence for this interpretation and further investigation to clarify this is needed.

The results of this study showed that the specialist species Clouded Apollo has increased its abundance and distribution in Estonia. The general trend for most European grassland butterflies and also elsewhere for *P. mnemosyne*, is a decline in abundance and distribution area (Kuussaari *et al.* 2007, Settele *et al.* 2008). Habitat loss, deterioration of habitat quality, increasing fragmentation of habitat patches or combined effects of all these factors are the main threats to Clouded Apollo (Meglécz *et al.* 1999, Luoto *et al.* 2001, Bergström 2005). In Estonia, the extinction of the subspecies of Saaremaa Island has most likely been related to habitat degradation in particular locations and a lack of other suitable habitats in the vicinity. Therefore, a possible explanation of the pattern of contrasting trends of Clouded Apollo in different geographical regions is availability and quality of suitable habitats. Similarly to other European countries, the traditional extensive agricultural practice is decreasing in Estonia. In general, the area of semi-natural grasslands in Estonia has decreased from 1,571,000 ha in 1939 to 130,000 ha in 2006 (Kukk & Sammul 2006). However, the area of specific semi-natural grasslands that are suitable habitats for Clouded Apollo still remains high. This is particularly notable in the case of semi-natural riparian meadows with strips of alders that are the preferred habitat for *C. solida* and Clouded Apollo in Estonia (Meier *et al.* 2005). Therefore, the increasing occupancy trend of Clouded Apollo observed in recent decades is likely to be associated with the fact that there is still a good availability of semi-natural grasslands, which are suitable for the butterfly. Additionally, Estonia has a good ecological network of natural communities and corridors, especially along rivers with riparian meadows that support the dispersal of Clouded Apollo. However, many suitable semi-natural grasslands are abandoned and have high risk of forest overgrowth, which could lead to higher pressure to the populations of Clouded Apollo in the future.

5. Conclusions

In this study, we provided an overview of the distribution of the threatened butterfly Clouded Apollo (*Parnassius mnemosyne*) in Estonia. During the last 30 years, the abundance and distribution area of Clouded Apollo has increased, except the subspecies on the island of Saaremaa has most probably gone extinct. On the other hand, a new record came from south-eastern Estonia in 1984, where the species had not been found previously. The exact reasons for the increase are unclear, but one can assume that the tendency is a combination of several factors, such as the presence of suitable habitats for the butterfly, the appropriate landscape structure with a sufficient density of habitat patches that support the dispersal of the butterfly. However, specific attention should be paid to avoiding the disappearance of suitable habitats of Clouded Apollo in the future.

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II

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Riparian buffer zones as elements of ecological networks: Case study on *Parnassius mnemosyne* distribution in Estonia

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Abstract

Territorial ecological networks (in US and some other countries known as greenways) are coherent assemblages of areas representing the natural and semi-natural landscape elements that need to be conserved, managed or, where appropriate, enriched or restored in order to ensure the favourable conservation status of the ecosystems, habitats, species and landscapes across their traditional range. An ecologically compensating areas network is a hierarchical system with the following levels: (1) core areas, (2) buffer zones of core areas, (3) corridors and stepping stones, and (4) nature development and/or restoration areas that support resources, habitats and species. Rivers form natural ecological networks and riparian buffer zones of rivers are typical elements of ecological networks. We studied the distribution of Clouded Apollo (*Parnassius mnemosyne*) and its habitat requirements in Estonia. Seventy-eight percent of all Clouded Apollo observations were recorded in riparian meadows along the banks of rivers with riparian strips consisting of bushes and trees. Detailed study showed that the butterfly is in most cases associated with meadows with a riparian strip of alder. This is the habitat of the food plant (fumeworth—*Corydalis solida*) of the larvae, the feeding and mating place of adults, and the migration and hiding site for the Clouded Apollo. The population area and number of individuals have been increasing during the last years, and a new growing South-Estonian sub-population of Clouded Apollo has also been discovered in Estonia.

Keywords: Clouded Apollo (*Parnassius mnemosyne*); Ecological network; Fumeworth (*Coridalis solida*); Migration corridors; Riparian buffer zones

1. Introduction

Territorial ecological networks are coherent assemblages of areas representing the natural and semi-natural landscape elements that need to be conserved, managed or, where appropriate, enriched or restored in order to ensure the favourable conservation status of the ecosystems, habitats, species and landscapes of regional importance across their traditional range (Bennett, 1998). According to a broader concept ecological networks (also called networks of ecolog-

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ically compensating areas) preserve main ecological functions in landscapes, such as: (1) accumulating material and dispersing human-induced energy, (2) receiving and transforming wastes from populated areas, (3) recycling and regenerating resources, (4) providing wildlife refuges and conserving genetic resources, (5) serving as migration-tracts for biota, (6) serving as barriers, filters and/or buffers for fluxes of material, energy and organisms in landscapes, (7) serving as a support-framework for regional settlements, (8) providing recreation areas for people, and, consequently, (9) compensating and balancing all inevitable outputs of human society (Mander et al., 1988).

Development of the idea of territorial ecological networks is largely based on the central place theory of von Thünen (1990), Christaller (1933, 1966) and Lösch (1954). Edgar Kant was the first who implemented the central place theory in explaining spatial economic relations on a country level. His monograph “Bevölkerung und Lebensraum Estlands” (Kant, 1935) presented several outcomes of this application in Estonia, including the hierarchical spatial structure of a landscape based on several different-order flows and influence fields considered simultaneously. Kant’s map of less populated areas of Estonia largely coincides with the modern ecological network schemes. Inspired by the *von Thünen–Christaller–Lösch* theory of central places and their hierarchy, Rodoman (1974) used the idea of influence pattern and spatial hierarchy for advancing the concept of polarized landscapes. According to this approach, two main poles – centres of human activities (e.g., cities) on one hand, and centres of pristine (undisturbed) nature (e.g., large forest and swamp areas) on the other hand – create the hierarchical gradient fields of interactions. Thus, it allows the use of the *von Thünen–Christaller–Lösch* model in the reverse direction, not proceeding from developing the economic, but the ecological benefit. In this case ecological benefit means, first of all, fewer disturbances by human activities. As an example of the combination of these two approaches, an idealized hexagonal model of rural landscapes was proposed by Mander et al. (1988) (Fig. 1), where landscapes with high human pressure (urban areas, fields) are buffered with compensative areas that form a proper network.

Based on long-term experiences, many countries in Europe have accepted the territorial ecological network as a hierarchical system with the following

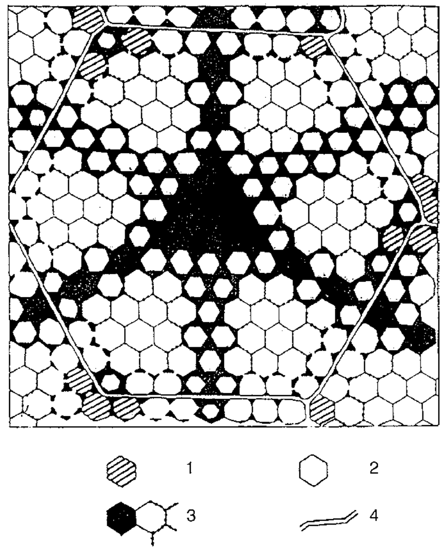

Fig. 1. Idealized hexagonal structure of a rural landscape as a principal model of ecological infrastructure and its hierarchy (Mander et al., 1988). 1: urban areas and settlements, 2: fields, 3: ecologically compensating areas (core areas and corridors with their buffers) and 4: main roads.

levels: (1) core areas, (2) buffer zones of core areas, corridors and stepping stones, and (3) nature development and/or restoration areas that support resources, habitats and species (Baldock et al., 1993). The size of network components serve as another criterion of the network’s hierarchy, having three levels (Mander et al., 1995): (a) macro-scale: large natural core areas (>1000 km^2) separated by buffer zones and wide corridors or stepping stone elements (width >10 km); (b) meso-scale: small core areas (10–1000 km^2) and connecting corridors between these areas (e.g., natural river valleys, seminatural recreation areas for local settlements; width 0.1–10 km); (c) micro-scale: small protected habitats, woodlots, wetlands, grassland patches, ponds (<10 km^2) and connecting corridors (stream banks, road verges, hedgerows, field verges, ditches; width <0.1 km).

As an example of designing the national-level ecological network, part of the Pan-European Ecological Network (PEEN) based on Estonian data from a 1 km^2

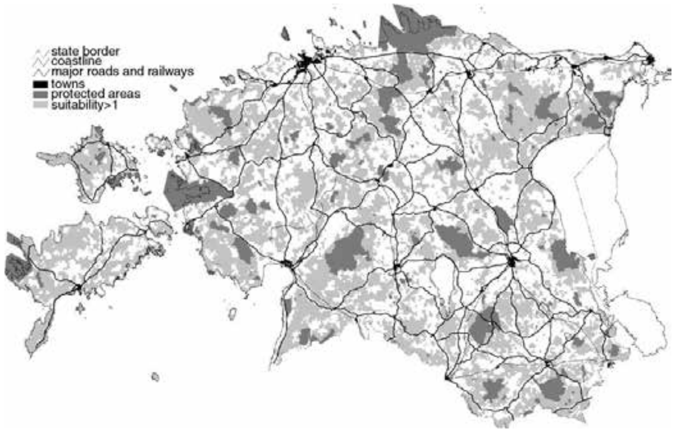

Fig. 2. Protected areas and areas not protected but suitable for inclusion in ecological networks according to their present natural state. The mean ecological network suitability value for Estonian land cover is 0.897, median 1.006; minimum value is −3.65 and maximum value is 3.75. The most common network suitability is between 1.0 and 1.5; the suitability value of protected areas is, as a rule, higher than that of non-protected areas (Remm et al., 2004).

grid is presented. The proposed ecological network design comprises of three principal layers: (1) general topographical features like coastlines, the water network, major roads, and place names for locating the depicted network, (2) a habitat-based field of suitability for the ecological network, calculated from network values of landscape features using a predefined algorithm, and (3) ecological network as an administrative decision. The second layer serves as a tool supporting decision making while the third layer consists of traditional components of an ecological network, like core areas, corridors, buffer zones, and nature development/restoration areas. Fig. 2 represents a combination of the last two layers as a map of protected areas (layer 3) and areas not protected but suitable for inclusion in ecological networks according to their present natural state (layer 2; Remm et al., 2004). Protected areas can be classified as core areas of ecological networks whereas the areas suitable for ecological networks can be considered as buffer zones and/or corridors.

Rivers with their tributaries create a natural system of "veins" which constitute a natural network through different communities and ecosystems, providing connectivity. Riparian buffer zones of rivers are typical elements of ecological networks, playing an important compensating role in all the hierarchical levels listed above. Also, their functions coincide with the idea of ecological networks. Most commonly, only filtering of polluted overland/subsurface flows and bank protection, as general functions of buffers, have been considered (Peterjohn and Correll, 1984; Vought et al., 1994; Kuusemets et al., 2001). In some papers the landscape aspects of riparian buffer zones have been pointed out (Lowrance et al., 1984; Vought et al., 1994). Some works have also highlighted the role of rivers and buffer zones in increasing longitudinal connectivity and biodiversity (Naiman et al., 1987; Farina, 2000), but this has been supported by few investigations. The main focus has been on the in-stream connectivity, e.g., in regard to fishes (Aarts et al., 2004; Koel, 2004) and water invertebrates (Sheldon et al., 2002; Aoyagui and Bonecker, 2004), but only few authors have dealt with riparian buffer zones and connectivity.

We studied distribution and possible migration of the Clouded Apollo (*Parnassius mnemosyne*) butterfly in riparian areas of Estonia, its dependence on the habitat type, and the role of riparian areas as migration corridors.

2. Materials and methods

All recorded occurrences and descriptions of Clouded Apollo (*P. mnemosyne*) in Estonia were collected and harmonized. The common database and the GIS was formed using MapInfo Professional 6.5, where every single description of the occurrence of Clouded Apollo was linked with the location on the digital cadastral map of Estonia (1:10 000). The description of land use type was made on the basis of the GIS.

In June 2003, a detailed description of the occurrence of Clouded Apollo in the middle part of the River Ahja was made. The number and sex of butterflies was estimated; the habitat was determined and described (dominant plants, presence of bushes close to the river, land use). Data were included in the common database; the area of habitats was measured and the density of butterflies in every habitat was calculated.

3. Results

There were 116 recorded occurrences of Clouded Apollo from 1903 to 2003 in Estonia. Most of them (85; 73%) are from the period 1990 and later; there were 12 (10%) from the 1980s and 19 (16%) from the earlier period. There are three main isolated populations of Clouded Apollo in Estonia: the population of Saaremaa Island, the North-Estonian population and the South-Estonian population (Fig. 3).

The Saaremaa population has not been recorded after 1973 and has probably become extinct. The first description of Clouded Apollo is from the year 1903 in North-Estonia. During first half of the previous century, all occurrences were locating only in the very east part of North-Estonia. Later the species expanded to the west and, especially during last 10 years, has been found in the valleys of several North-Estonian rivers. The South-Estonian population was first described in 1985 and has been increasing rapidly since this time in territorial spread and in the number of individuals.

Of all the occurrences of Clouded Apollo, 15 (13%) have been located on the banks of lakes, 10 (9%) in the coastal area of the Baltic Sea and all the rest (91; 78%) in the riparian areas of rivers. The dominating land cover type was meadow with a riparian strip of bushes and trees close to the riverbank. This habitat type was found in about 60% of the described sites of Clouded Apollo. Thirty percent were meadows and 10% were wet meadows that both were predominantly situated between meadows with a riparian strip of bushes.

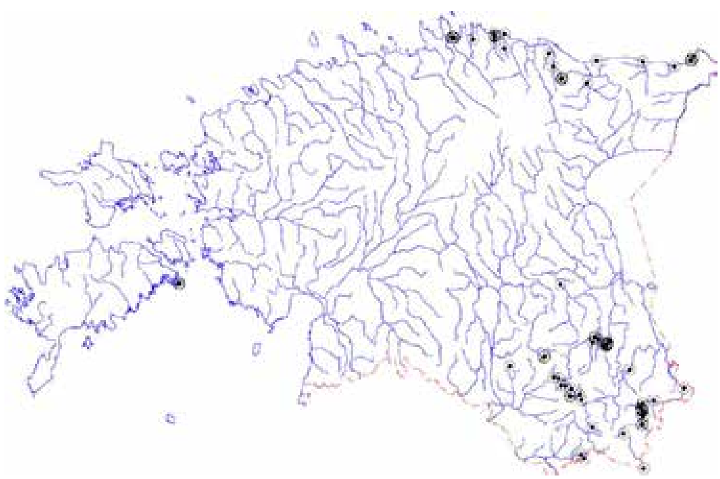

Fig. 3. Distribution of Clouded Apollo (*Parnassius mnemosyne*) in Estonia.

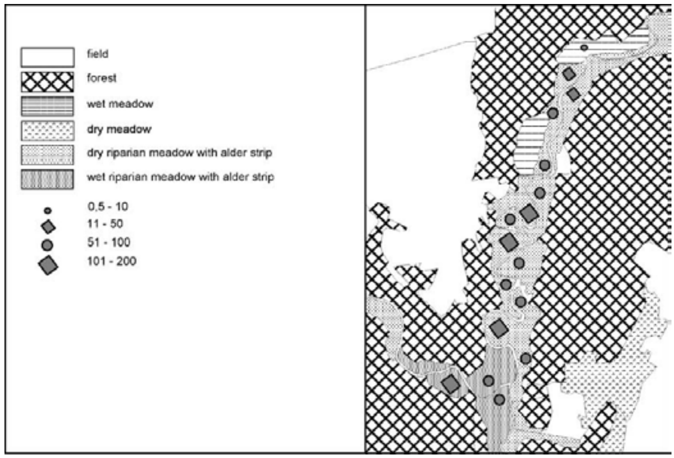

Fig. 4. Habitat type structure and density (individuals per hectare) of Clouded Apollo (*Parnassius mnemosyne*) in the Ahja River valley, South Estonia.

Also, the detailed study showed that the Clouded Apollo is mainly associated with dry riparian meadow with a strip of alders (*Alnus incana*), since 13 habitats of this kind from a total 17 were populated with the butterfly (Fig. 4). The density of butterflies was as high as 200 individuals per hectare in three meadows with an alder strip and was in most cases between 51 and 100 individuals per hectare. In wet meadows, the Clouded Apollo was found in four cases.

4. Discussion

The Clouded Apollo, a protected species according to EU Directive Natura 2000, has special requirements regarding habitat. Clouded Apollo larvae are dependent on a single plant species, since they feed only on the leaves of fumewort (*Corydalis solida*). This plant grows at the sunny margins of forests and trees in wet conditions, but does not grow in permanently flooded places, wetlands, and on hummocks.

The imago of the Clouded Apollo requires open meadow for mating and as a habitat for its food nectar plants (Meglécz et al., 1999; Välimäki and Itämies, 2003). At the same time, this relatively large butterfly is sensitive to high wind speeds. Therefore, they fly short distances, between trees, and avoiding large open areas. A study in Finland (Luoto et al., 2001) showed that the presence of Clouded Apollo was significantly dependent on the number of fumewort plants, on the heterogeneity of landscapes, and on the presence of semi-natural grasslands, deep valleys, and areas with low wind speed. In Estonia, these kinds of conditions are met in the riparian communities of rivers, especially in meadows with strips of bushes and trees that support the migration of Clouded Apollo and provide shelter against the wind. The results of the detailed study on the River Ahja showed that this butterfly is to a great extent associated with riparian meadows with riparian strips of alder. This is a typical riparian tree in Estonia and the understorey of the narrow riparian alder strip close to water table is the main habitat for fumewort. Therefore, the Clouded Apollo is mainly found in dry riparian meadows with an alder strip since this habitat is the main habitat of the food plant of the larvae of Clouded Apollo and the main feeding and mating habitat of the adult and since this habitat provides suitable migration and hiding places for the adult butterfly. Occurrences of Clouded Apollo are mainly situated along the banks of rivers.

Despite the fact that the numbers of Clouded Apollo are decreasing in most areas of Europe (Meglécz et al., 1999; Välimäki and Itämies, 2003), the population area and the number of individuals are increasing on the population's northern distribution boundary. This has been discovered in Finland and Karelia (Humala, 1997) and has now also been discovered in Estonia, where Clouded Apollo is occupying new territories and increasing in numbers. Our results show that there is an overall increase in the numbers of Clouded Apollo in Estonia, since 73% of all occurrences have been recorded during the last 13 years. Also, a new population has been found in South-Estonia, which is rapidly increasing in numbers and in territory. The exact reasons for this increase in Estonia are unclear, but one precondition is the presence of suitable habitats for the butterfly. This kind of habitat is linked to traditional agricultural practices such as hay making and grazing of cattle and sheep. However, during the last few years these agricultural practices have decreased considerably and former meadows are overgrowing. There is also pressure to cut down riparian bushes and trees. This all can lead to the loss of habitats for Clouded Apollo.

5. Conclusions

Territorial ecological networks represent a new paradigm in nature conservation and landscape planning. The crucial parts of the network are connecting corridors and stepping stones. Riparian communities of rivers can be considered to be important elements in territorial ecological networks since rivers create natural networks in landscapes.

The study of Clouded Apollo showed that it appears in most cases along river valleys in the riparian meadows with alder strips, since this kind of habitat is also the one required by fumewort—the food plant of Clouded Apollo larvae; this habitat is the main feeding and mating place and migration and hiding site for the butterfly. The protection of Clouded Apollo primarily needs the protection of this complex habitat, including continuing traditional land use in the area and preservation of riparian alder strips on river banks.

Although the landscape aspects of riparian buffer zones and their role as connecting and migration corridors have been pointed out in several papers, a general concept regarding landscape planning and management should be developed.

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III

Kuusemets, V., **Kask, K.**, Liivamägi, A., Luig, J., Kaart, T.,
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THE HABITAT PREFERENCES AND RANGE EXPANSION
OF THE CLOUDED APOLLO BUTTERFLY
PARNASSIUS MNEMOSYNE (L.) IN ESTONIA.

Submitted.

The habitat preferences and range expansion of the Clouded Apollo butterfly *Parnassius mnemosyne* (L.) in Estonia

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Abstract

The Clouded Apollo (*Parnassius mnemosyne*) is an endangered butterfly species that has declined in range and abundance throughout most of Europe. In Estonia, however, the species exhibits opposite trends. Since 1984, a new population has become established in South Estonia that has increased its abundance and expanded its range relatively rapidly. We studied the possible reasons for this phenomenon and found that the primary reasons may be the availability of high quality habitats and a supporting landscape structure with rivers as migration corridors. The favoured habitat of the Clouded Apollo was semi-natural meadows with strips of alders (*Alnus incana*), which were also the primary habitat of the larval food plant, *Corydalis solida*. The optimal habitat patch size for the Clouded Apollo was 1 to 3 ha. The species dispersed into new regions and populated a large area in South Estonia, moving at a rate of up to 75 km over a 10-year period.

Keywords: butterflies, migration corridors, distribution, patch, landscape, *Corydalis solida*

Introduction

The Clouded Apollo [(*Parnassius mnemosyne* (L.)] is a threatened species protected by the Bern Convention, the EU Habitat Directive Natura 2000 (CEE Habitat Directive 43/92, Annex IV) by several national protection acts and is included in many regional Red Data Books. The Clouded Apollo is a specialist species with specific habitat-butterfly relations, whose larvae are monophagous on *Corydalis* spp. The butterfly inhabits heterogeneous habitats in small isolated patches (Välimäki & Itämies 2003, Gorbach & Kabanen 2010) that are typical of metapopulations (Hanski & Thomas 1994). Therefore, the butterfly has been of interest to several scientists. One of the primary interests has been the degree of isolation and mobility of the Clouded Apollo, which has been studied primarily using the mark-release-recapture (MRR) method (Konvička & Kuras 1999, Meglécz et al. 1999, Välimäki & Itämies 2003, Gorbach & Kabanen 2010). All studies have found that the Clouded Apollo butterfly is a sedentary species that moves relatively short distances. For example, Gorbach & Kabanen (2010) found that the average movement distance of the Clouded Apollo was 120 m and the maximum movement distance was 2.68 km; Välimäki & Itämies (2003) and Konvička & Kuras (1999) determined similar values of 142 m and 1.35 km, and 232 m and 2.55 km, respectively. However, the actual movement potential of the Clouded Apollo may be much greater, and could reach several tens of kilometres by the end of its life cycle (Gorbach & Kabanen 2010). To date, this has not been documented by scientific studies.

Our study on the distribution changes of the Clouded Apollo (Liivamägi et al. 2013) showed that the range and abundance of this butterfly has increased remarkably during recent decades in Estonia. Originally, the Clouded Apollo was found only in Northeast Estonia (the population on the island of Saaremaa probably became extinct in the 1970s). In 1984, individuals of the Clouded Apollo were found in Southeast Estonia. The analysis of distribution changes showed that the butterfly has since increased its range by over 50 km from the locations of first sighting during a 10-year period. The reasons for such a rapid expansion are unclear.

Therefore, in the present paper we analyse the movement of the Clouded Apollo in the South Estonia population, and the possible impact of habitat quality, habitat size and landscape structure on the distribution of the butterfly. We suggest that the reason for this range expansion of the Clouded Apollo may be the presence of suitable landscape structure with suitable habitats situated along the riverbanks, which function as connecting corridors between potential habitat patches. There are several studies showing the importance of landscape structure and connecting corridors for the movement of butterflies (Dover et al. 1997, Haddad 1999, Brückmann et al. 2010, Öckinger et al. 2012). However, more data are available on the movements of butterflies within and between habitat patches, and less is known of their use of biotope (linear) corridors and gateways (Dennis et al. 2013). Some authors note that the importance of corridors could be species and landscape specific (Collinge 2000, Dover & Settele 2009). Corridors appear to be more important for butterflies in forested landscapes than open landscapes (Öckinger & Smith 2008). Konvička et al. (2007) found that the vertical structure of forest edges is an important factor influencing the movement of the Clouded Apollo. Sharp edges with tall coniferous trees are less favourable for the Clouded Apollo than shorter forest mantles with deciduous trees and bushes. This finding indicates a need to analyse more precisely the effects of habitat quality, corridors and barriers, including the vertical structure of the surrounding biotopes, on the Clouded Apollo butterfly.

Methods

We collected all known records of sightings of the Clouded Apollo from the South Estonia population. The records of sightings are taken primarily from the national periodical publication *Lepinfo* issued by the Estonian Lepidopterologists' Society, and the section for entomology of the Estonian Naturalists' Society, which has collected most sightings of butterflies in Estonia since 1981. In addition, data were obtained from two major butterfly collections in Estonia—the Natural History Museum of the University of Tartu, and the entomological collection of the Department of Zoology, Institute of Agricultural and Environmental Sciences, at the Estonian University of Life Sciences. Finally, unpublished data from entomologists and data from the field work of authors on the current paper (from 2002 – 2012), were added. The data from *Lepinfo* are given in 10x10km UTM quadrates along with the name of the location of the sighting. Most sightings of butterflies by entomologists and in our fieldwork were determined by GPS. Therefore, in most cases, the locations of the sightings describe exact patches or habitats of the butterfly; in the remaining cases, the accuracy the data is within at least 1 km. All data were unified and a common map-based GIS database was created. The database was created, and movement distances and land cover data were analysed using the software program MapInfo Professional 10.0.

We studied the abundance of the Clouded Apollo and the distribution of *Corydalis solida* in the largest subpopulations of the butterfly, located in the central Ahja River valley and in the Piusa River valley. The distribution of *Corydalis solida* in the area of the subpopulations was mapped at the end of April and beginning of May of 2004 and 2005, during the most active flowering period of the plant. Both banks of the rivers and their surrounding areas were checked continuously; all observations of the flowers were recorded on the map and included in the GIS database. The number of butterflies was determined during the first half of June around the midday, on days with sunny weather, temperatures above 16° C and wind speeds of less than three on the Beaufort scale. The number of Clouded Apollos was counted, and the habitat type of patches (n=16) was described for Ahja River subpopulation. The butterfly was found in 3 types of habitats: dry semi-natural meadows, dry semi-natural meadows with a strip of trees and wet meadows with a strip of trees. The semi-natural meadows in Estonia are species-rich meadows with several flowering species that are good sources of nectar for butterflies. We calculated the area (ha) and perimeter (m) of the patches from the Estonian digital basic map (1:10,000) provided by the Estonian Land Board. We used single-factor dispersion analyses and regression modelling to determine if there was any statistically significant relationship between meadow patch area/perimeter and abundance of Clouded Apollos. The analyses were performed with the statistical software STATISTICA 9, and significance was assigned at $p < 0.05$.

In both subpopulations of Clouded Apollo, Ahja River valley and Piusa River valley, the vertical structure of the surrounding land cover types was assessed by openness of surrounding landscapes. We used a digital CORINE land cover map (1:100,000) as a more generalised land cover map available for Estonia, and gave 'openness values' to the different land cover types surrounding butterfly habitats. We used surface roughness values, which are used to assess wind speed in different biotopes and are based on the height of vegetation (Troen & Petersen 1989), and adapted them to the CORINE land cover classes (Kull 1996). Using surface roughness, we divided land cover types into 5 classes where lower values (<0.2) indicated more open areas (e.g., grasslands) and higher values (0.8–1.0) indicated taller closed areas (e.g., coniferous forest, Table 1). Using these classes, a map of the openness of land cover types adjacent to the habitats of Clouded Apollos was created with MapInfo Professional 10.0.

Finally, in all subpopulations where the exact position of butterflies was known, we calculated the average distance of butterflies from water bodies, with an accuracy of 5 m.

Table 1. Values of openness and surface roughness of CORINE land cover classes (Kull 1996).

Openness value	Code and name of CORINE land cover classes		Roughness value
0-0.2	4111	Inland marshes	0.1
	4122	Natural peat bogs with scattered trees and shrubs	0.03
	321	Natural grasslands	0.1
	211	Non-irrigated arable land	0.1
	4112	Open fens and transitional bogs	0.03
	231	Pastures	0.1
	122	Road and rail network	0.1
	333	Sparsely vegetated areas	0.05
	4121	Explored peat bogs	001
	512	Water bodies	0
	511	Water courses	0
0.2-0.4	334	Burnt areas	0.3
	242	Complex cultivation patterns	0.3
	133	Construction sites	03
	132	Dump sites	0.3
0.4-0.6	112	Discontinuous urban development	0.5
	222	Gardens	0.5
	121	Industrial or commercial units	0.5
	243	Land principally occupied by agriculture	0.5
	322	Moors and heathland	0.5
	3241	Transitional woodland /scrub on mineral soil	0.5
	3242	Transitional wood-land/scrub on mire	0.5
0.6-0.8	311	Broad-leaved forest	0.7
	141	Green urban areas	0.7
	142	Sport and leisure facilities	0.6
0.8-1.0	312	Coniferous forest	1
	111	Continuous urban development	1
	313	Mixed forest	0.8

Results

The first sightings of the Clouded Apollo in Southeast Estonia were recorded between 1984 and 1986, from 4 different locations close to the Estonian border; these locations were separated from each other by 9–22 km. This indicates that the dispersal of the butterfly to Estonia took place several times from a larger population in Russia. During subsequent years, the number of butterflies increased and formed a vital subpopulation in the Piusa River area. In successive years, the butterfly moved relatively rapidly into new areas. In 1990, the butterfly was found along the central Ahja River, 40 km from the line of first sightings (Fig. 1). This new subpopulation maintains a large number of individuals to the present day. In 1993, 10 years after first sightings in Southeast, the butterfly was found 75 km away in the area of Puka. The Puka subpopulation, however, is now more fragmented, except near the Elva River valley. In 1995, the butterfly was found in the Võhandu River valley, located up to 55 km from the line of first sightings, and remains a significant subpopulation.

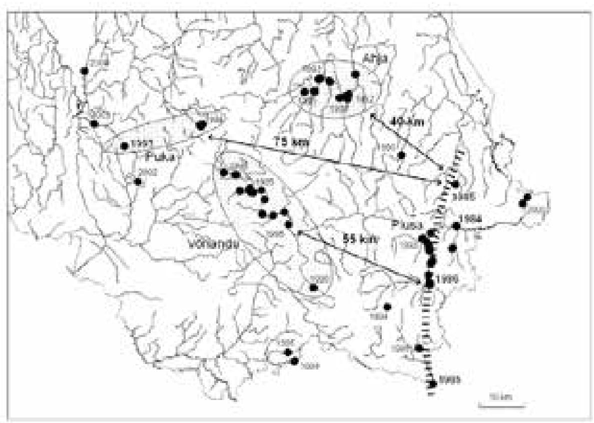

Figure 1. The distribution of the Clouded Apollo in South Estonia since 1984. Place names indicate name of subpopulation, years indicate year of sighting, horizontal bars indicate line of first sightings, and arrows indicate maximum distance from the line of first sightings.

The analysis of surrounding land cover showed that the butterfly is found in narrow river corridors with riparian meadows between tall forests (Fig. 2). These meadows have narrow strips of riparian trees on the banks of the rivers that consist primarily of grey alders (*Alnus incana*), which are the most common riparian tree in Estonia. Some single trees of *Prunus padus*, *Fraxinus excelsior* and other deciduous trees and bushes are found in the strips. The riparian strip of alders is also the primary habitat of the fumewort (*Corydalis solida*) in Estonia—the larval food plant of the Clouded Apollo, which grows in a narrow strip several meters wide under the alders, near the meadows. The fumewort was ubiquitous in the studied areas within the river valleys (Fig. 2).

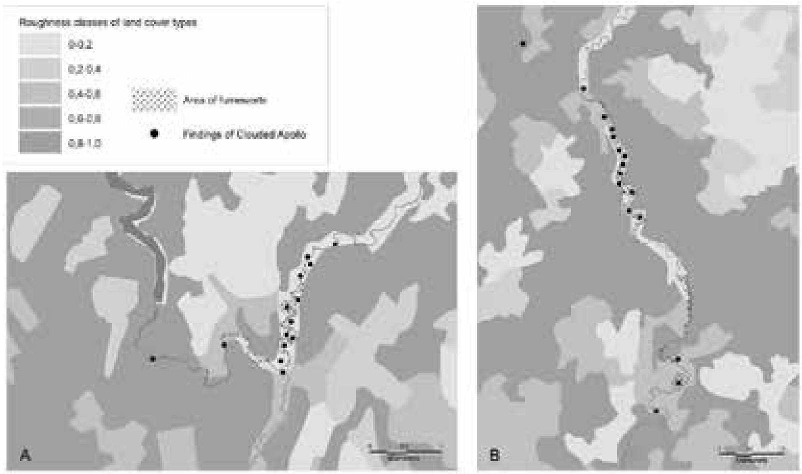

Figure 2. The openness of surrounding land cover types, and the location of butterflies and fumeworts in the Ahja River (A) and Piusa River (B) valley subpopulations of the Clouded Apollo.

The Clouded Apollo was primarily observed flying close to the riparian strip of alders. The butterfly was typically found flying 10–150 m from rivers (92% of all sightings, Fig. 3), usually within 10–50 m (73% of sightings).

The most densely populated habitat of the Clouded Apollo was dry semi-natural meadows with a strip of riparian trees (11 of 16 cases, Table 2). The number of butterflies ranged from approximately 40 to 300 individuals on these patches. Wet meadows with a strip of trees were occupied by the Clouded Apollo in 3 cases and dry semi-natural meadows without trees were occupied in 2 cases.

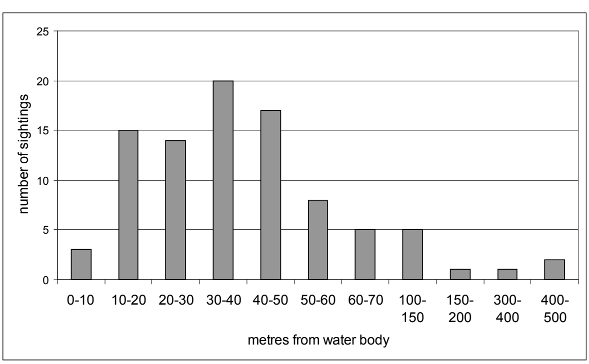

Figure 3. Distances of the Clouded Apollo butterflies from water bodies (m).

Due to the relatively low number of patches studied, the relation between abundance and habitat types was not statistically significant by single-factor dispersion analysis (*p*=0.226; Table 2). Similarly, the relations between abundance and area, and abundance and perimeter of patches were not statistically significant: *p*=0.162 and *p*=0.980, respectively.

Table 2. Mean abundance of Clouded Apollos (standard deviation), area of patches (ha) and perimeter of patches (m) in different habitat types; *p*-value shows the level of significance among the habitat types (dispersion analysis).

Habitat type	number	abundance (individuals)	area (ha)	perimeter (m)
dry meadow with strip of trees	11	155.5 (104.7)	1.95 (0.89)	743.0 (287.0)
dry meadow	2	110.0 (42.4)	1.52 (0.49)	783.9 (312.7)
wet meadow with strip of trees	3	250.0 (0.0)	2.97 (0.93)	740.2 (157.7)
p-value		0.226	0.162	0.980
Total	16	167.5 (96.64)	2.09 (0.93)	747.6 (254.85)

Linear regression models showed statistically significant relationships between butterfly abundance and the size of patches (R^2=0.377; *p*=0.011; Fig. 4) and no significant relationship between abundance and the perimeter of patches (R^2=0.074; *p*=0.308; Fig. 5). Quadratic regression models showed statistically significant relationships between butterfly abundance and the size of patches (R^2=0.538; *p*=0.007) and butterfly abundance and the perimeter of patches (R^2=0.509; *p*=0.010). This suggests that there might be an optimal habitat size for the butterfly populations.

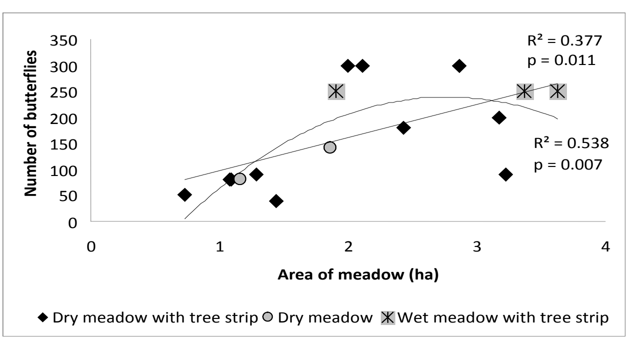

Figure 4. Regression analyses between abundance of Clouded Apollos and area of patches (ha).

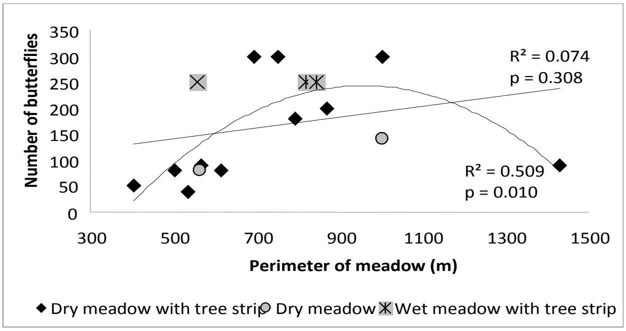

Figure 5. Regression analyses between abundance of Clouded Apollos and perimeter of patches (m).

Discussion

The South Estonia population of the Clouded Apollo occupied a relatively large area over a relatively short time. Our aim was to analyse conditions that led to this phenomenon. The success of the Clouded Apollo in Estonia may be the result of proper landscape structure and well-structured, high quality habitats; i.e., species-rich semi-natural meadows on the banks of rivers, with riparian strips of bushes and trees that are well connected and create migration corridors and stepping stones for butterflies. Butterflies in general are dependent on species-rich meadows that provide nectar sources. Several studies have found that the abundance and species richness of butterflies is dependent on the abundance and richness of nectar plants (Luoto et al. 2001, Pywell et al. 2004). Meadows are also important places for mating and breeding of the Clouded Apollo (Välimäki & Itämies 2003, Bergström 2005).

Butterflies may benefit from forest edges that provide several favourable conditions (Liivamägi et al. 2014). For large and poor-flying butterflies such as the Clouded Apollo, one very important habitat requirement is shelter (Dover et al. 1997, Pywell et al. 2004, Rosin et al. 2012). For this reason, the Clouded Apollo is often observed flying close to the forest edge; they fly particularly close to shorter deciduous forests and bushes, which are very important for the movement of Clouded Apollos, whereas taller coniferous trees can present a barrier to the butterfly (Konvička et al. 2007). Our study confirmed that the butterfly was primarily found close to riparian strips with deciduous trees and bushes; in 73% of cases, the butterflies flew 10–50 m from the water body within the riparian strip. However, shelter may be not the only reason the butterfly is flying close to the riparian strip. As a monophagous butterfly, the Clouded Apollo is also dependent on the food plant of the larvae (Konvička & Kuras 1999, Luoto et al. 2001, Bergström 2005). In Estonia, the larvae feed on *C. solida*, which grows on the banks of rivers under a relatively narrow strip of trees, primarily alders (Meier et al. 2005). It is possible that the Clouded Apollo is remaining close to the deciduous trees and bushes while they track the habitat features of the larval food plant during egg laying because the food plant is neither flowering nor growing (Konvička et al. 2007). Most of the butterfly habitats coincided with the distribution area of *C. solida*. The most frequent habitat type (69%) for the Clouded Apollo was dry semi-natural meadows with a riparian strip of alders and bushes, which was also the habitat of *C. solida*, and the butterfly was typically found close to the strip of alders. The importance of deciduous forests for the Clouded Apollo has also been stressed by other authors (Luoto *et al*. 2001, Välimäki & Itämies 2003, Heikkinen *et al*. 2007, Gorbach & Kabanen 2010).

The analysis of openness of surrounding landscapes in the Ahja River and Piusa River subpopulations showed that the butterfly was found in narrow corridors of meadows surrounded by tall forests, primarily pine forests. In the centre of the corridor was the river with the strip of alders, where most of the *C. solida* and butterflies were found. Although there were other nectar-rich meadows in the area, neither butterflies nor *C. solida* was found in these biotopes.

In general, the abundance of butterflies increases with the size of patches (Krauss et al. 2003, Öckinger et al. 2012). However, different species may require different patch sizes, particularly specialist species (Dover & Settele 2009, Rosin et al. 2012). In our study, the meadows on the banks of rivers were relatively small, and the number of Clouded Apollos showed the greatest abundance in habitats of 1–3 ha, which appears to be the optimal habitat size for this butterfly. This small patch size can be explained because larger habitats are more open, and the Clouded Apollo requires forest edges and strips for the habitat of the food plant, and as shelter for movement.

Therefore, the combination of semi-natural meadows as nectar sources and mating places for the imago, rivers as open movement corridors, riparian strips as places for shelter and habitat for the monophagous larvae food plant, constitutes high quality habitat for the Clouded Apollo.

This availability of high quality habitat may be the reason why the butterfly has dispersed relatively rapidly in South Estonia. Although the Clouded Apollo is considered to be a sedentary species (Välimäki & Itämies 2003), in our study, the butterfly moved a straight-line distance of up to 75 km over 10 years, and 40 km over 6 years, for a rate of approximately 6.5 to 7.5 km a year. Because the movement assessment is based on sightings and we did not have continuous monitoring of the butterfly during this time, these numbers should be discussed. Dates of sightings probably vary from the time of actual movement, but they are probably reliable because the areas were visited frequently by entomologists; the Piusa and Puka areas, in particular, were visited regularly, and this butterfly always receives ample attention. In addition, the butterfly does not disperse in a linear manner. It is possible that the Clouded Apollo first moved to the Võhandu area and from there to Puka because the Võhandu valley was only area poorly studied during these years; this would make the movement route kilometres longer. The rapid expansion of the Clouded Apollo is supported by the observation, in 2005, of the butterfly 145 km west of the location of first sightings in Southeast Estonia. This contradicts the MRR studies, which document small movement distances for this butterfly. One important factor may be the size of the dispersal study area. Franzén and Nilsson (2007) found that realistic estimates of dispersal distance require a study area at least 50 km^2. This simple study of sightings can describe the distribution of the species more precisely over a longer period and a larger area than MRR studies.

Conclusions

The abundance and range of the Clouded Apollo has increased in recent years in Estonia, which is the opposite trend of that observed in the rest of Europe. The reason for this increase appears to be the availability of ideal, high quality habitats with ideal landscape structure for the Clouded Apollo, i.e., riparian semi-natural meadows with strip of alders. These habitats offer nectar plants and mating sites for the butterfly, well-structured habitat with trees that provide shelter from the wind and habitat for *C. solida*, the food plant of the larvae, and together with the river valley, they create a suitable migration corridor for the butterfly.

The Clouded Apollo is a species that clearly benefits from corridors in the landscape that increase their mobility. In Estonia, such natural corridors are formed by rivers, which provide connectivity between isolated patches of metapopulations, and may make an important contribution to the distribution of the butterfly. However, attention is needed to avoid overgrowth of these meadows and to ensure the necessary density of suitable habitats that create stepping stones and corridors for the species.

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IV

Meier, K., Kuusemets, V. & Mander, Ü. 2005.

SOCIO-ECONOMIC AND LAND-USE CHANGES IN THE PEDJA RIVER CATCHMENT AREA, ESTONIA.

River Basin Management III. WIT Transactions on Ecology and the Environment. WIT Press. Vol 83: 585–592.

Socio-economic and land-use changes in the Pedja River catchment area, Estonia

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Abstract

During the last 15 years, large-scale socio-economical changes have occurred in Estonia. This has been influencing agricultural activities and has resulted in land-use changes with ecological consequences. The relative share of agriculture in GDP has dropped from 19% to 3.1 during the last 20 years, the number of people employed in agriculture has decreased from 136 800 to 31 500 during the last 15 years. This has caused a loss of jobs and the abandonment of agricultural land. The biggest change in land use has been the overgrowing of ecologically valuable wooded meadows, floodplains, alvars, and natural grasslands. The area of wooded meadows has decreased from 850 000 ha in the 1940s to 800 ha at present. Also, in the community of Puurmani, the human population has dropped 11% during the last 3 years. Agricultural activities have declined significantly; the number of pigs has decreased 24 times and the number of cattle, 1.6 times during last 15 years. 514 ha of former flooded meadows and wooded meadows of River Pedja have reverted to forest and 33 ha to dense bush at present.
Keywords: biodiversity, flooded meadows, land-use changes, socio-economic changes, wooded meadows.

1 Introduction

During the last years, considerable socio-economic changes have occurred in the whole of Europe. For Eastern European countries these changes have been remarkable during the last 15 years as a result of political changes. At the beginning of the 90s a rapid change in the political system, from Soviet Socialist Republic to the independent state of Estonia, took place, which gave new opportunities for the development of the country. This included ownership changes, which in rural areas meant the liquidation of the old system of *kolkhozes* and *sovkhozes,* which were replaced with small private farms and cooperative farms. Also, agriculture as a whole had to refocus from the eastern to the western market, in a situation where, during first years of independence, agriculture was not subsidised by the state. This resulted in a considerable decrease in agricultural production, loss of jobs, and finally in the set-aside of agricultural land.

These fast socio-economic changes resulted in several ecological consequences that, in some cases, have had a negative impact to ecosystems. Especially rapid changes took place in old traditional semi-cultural landscapes with extensive cultivation (mowing, grazing) like wooded meadows, alvars, and coastal and riparian meadows, which have high ecological value and increase the heterogeneity of the landscape. For example, wooded meadows in Estonia have very high plant diversity: up to 74 species per one m^2, which is one of the highest in Europe [1]. Wooded and alvar meadows are rich in butterflies including several species protected by EU Directive *Natura 2000* (*Euphydryas aurinia*, *Coenonympha hero*, *Lopinga achine*, *Lycaena dispar*). Likewise, the number of bumblebee species has been found to be higher in semi-natural areas than in agricultural areas of Estonia [2]. The extensive management of grasslands also increases the number of other insects like grasshoppers, bees and wasps [3]. Flooded meadows, riparian meadows and buffer strips have a high ecological value, since they increase biodiversity and create important migration corridors in landscapes [4]. In Estonia, many valuable species, such as dragonflies (*Aeshna viridis*, *Ophiogomphus cecilia*), hermit beetle (*Osmoderma eremita*), are linked to riparian habitats along rivers. Also, the protected butterfly, Clouded Apollo (*Parnassius mnemosyne*) is related to such a habitat, since 78% of all observed occurrences of Clouded Apollo in Estonia have been registered in the riparian meadows of rivers [5].

According to the Estonian Red Book, the overgrowth of semi-cultural landscapes is a threat to 7 mushroom, 23 lichen, 80 plant and 23 animal species in Estonia [6]. Meadow habitats are also important constituents of protected areas, constituting 10% of all the protected areas in Estonia.

Therefore, socio-economic changes in rural areas can have a direct impact on the ecosystems and the ecological value of landscapes. This paper deals with general socio-economic changes in rural areas of Estonia and with the related land-use changes in one rural municipality in more detail.

2 Material and methods

2.1 The socio-economic analyses

The analyses of socio-economic changes were made using the database of the Statistical Office of Estonia (SOA). The analyses of land-use changes were made by comparing Estonian cadastral maps from the 1930s and from the beginning of the 1990s.

2.2 Location and natural conditions of the Puurmani community

The Puurmani community is situated in the central part of Estonia, in the southwestern part of Jõgeva County (Fig. 1).

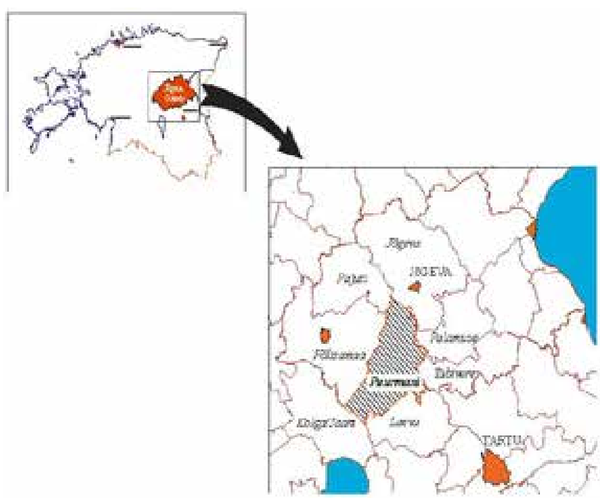

Figure 1: Location of the Puurmani community.

The territory of the Community is 292.7 km^2, which is slightly bigger than the average area of Estonian rural municipalities – 212 km^2. The central village of the rural municipality – Puurmani, is situating 27km from the county centre – Jõgeva; 38km from the second largest town in Estonia – Tartu and 150km from the capital of Estonia – Tallinn.

The Puurmani community is in the transition zone between Estonia's two contrasting bedrock types. The whole municipality and all of Northern Estonia lie on limestone bedrock; Southern Estonia, South from Puurmani, lies on sandstone. This dictates the characteristic conditions for the soils of the municipality. The limestone bedrock is covered with a thin (1-3m) sandy-loam moraine layer and with calcareous soils, forming flat landscapes. Soils of the community are mainly podzolic soils that, in the case of moderate moisture conditions, have high fertility; however most of the soils are humid or wet and are suitable for agriculture only after drainage. In the western part of community the bedrock is covered with clay sediments topped with peatlands. In the floodplains of rivers, wet peat soils can be found. The eastern and central part of the community is covered with soils suitable for agriculture, which have a relatively high quality (55 points from maximal 100, according to the local soil quality scale) for Estonian conditions (40 is the average for Estonia; less than 35 is considered not suitable for agriculture) [7].

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In the western part of the community is situated a large wetland system that, from 1952 until 1991, was a Soviet Air Force bombing practice area. In 1994, the Alam-Pedja Nature Protection area was established in this area and is included in the list of Ramsar sites. 82% of the protection area is wetland, its total area is 260 km^2. The Emajõgi, Pedja and Põltsamaa rivers flow through the protection area; their flooding area in spring time can reach 92km^2, which creates valuable habitats of European importance.

3 Results and discussion

3.1 Socio-economic changes in Estonia

During the last 10-15 years, tremendous structural changes in agriculture have taken place in Estonia. The re-orientation of agriculture to the new economic conditions has resulted in the marginalisation of rural areas.

The relative share of agriculture in Estonia's GDP dropped from 19% in 1984 to 5.8 in 1997 and finally to 3.1% in 2002 [8]. The re-structuration of the economy did not take place so fast, the unemployment rate increased, agricultural land was set aside, nearly 25% of arable land was temporarily disused and many people moved away from rural areas. According to the SOA, the population has dropped 10-40% in 83 rural municipalities and 0-10% in 80 municipalities, from a total of 416 municipalities, during the last ten years. In 1960, 25.4% of all employed people were employed in agriculture; in 1980 this number was 13.5, and in 1996, 8.1%; in 2000 this figure fell to 5.2%. In just one decade the number of people employed in agriculture decreased from 136 800 in 1990 to 31 500 in 2000.

The number of cattle and pigs dropped during ten years to the pre-Second World War level [8]. New economic activities did not replace agriculture as rapidly as expected, although many people moved out to the bigger cities and industrial centres.

Large changes have occurred in land use through the whole century. The area of forest has increased almost three times from 1940 to 2000. This is mainly due to a large decrease in the area of natural grasslands, most of the grasslands being overgrown by forests. In contrast, the area of arable land has been fairly stable through the century [9]. At the beginning of the 19th century, the area of wooded meadows comprised 850 000 ha, a level similar to that before the 1940s. Today about 800 ha of wooded meadows remain and cutting of hay is taking place only on 200 hectares [6].

3.2 Socio-economic changes in the Puurmani community

The population of the Puurmani community on 01.01.2003 was, according to SOE, 1904, which is close to the average number – 2244, for Estonian rural municipalities. In 1959, there were 2577 people living on the territory of present-day Puurmani community, and that number has decreased steadily over 50 years. A larger change took place in between 1959 and 1979, when the population decreased from 2577 to 2137; this was followed by a more stable period until 2000. Rapid change has been taking place during short period 2000 to 2003, when the population decreased about 11% from 2145 to 1904. Although, the share of the old people in the community is high, and natural population growth has been negative during the last years (2 to 12 people per year) it is still very small in comparison with the total decrease of the population due to migration away from the area. Also, the number of people working outside of the community has increased rapidly during the last years, from 150 in 1997 to 250 in 2000 [7]; this may lead to their eventual migration away from the municipality. This pressure is caused by the general difficulties in the agricultural sector, lack of professional jobs in the area and the strong impact of neighbouring cities.

3.3 Land-use changes in the Puurmanni community

Agriculture has been the main economical activity in the area for many years. One kolkhoz and one sovkhoz were sited within the territory of the present Community. Their highest level of production was at the end of the 1980s; after this, agricultural production has been decreasing steadily. As a result, the number of pigs has decreased 24 times during the period 1989 to 2001 and the number of cattle, 1.6 times, both being even lower than that before the War (Table 1), even though the data from 1939 was from a much smaller area than that from 1989 and 2001. Also, the kolkhoz and sovkhoz did not farm sheep and poultry in 1989, but these animals were quite often bred in family farms that were not represented in the statistics of the time.

Table 1: Number of animals in the Puurmani Community in 1939-2001.

	1939*	1989**	2001***
Number of cattle	2696	4581	2879
Number of pigs	1817	7261	301
Number of sheep	2145	-	6
Number of poultry	7549	-	3099

* in the Kursi Community, which constituted about 65% of the area of the present Puurmani Community (Estonian Statistics, 1939)
** kolkhoz “Rahva Hääl” and sovkhoz Sadukϋla [10]
*** according to the agricultural counting, database of SOE.

The most drastic change has taken place in the number of sheep: from 2145 before the war to 6 in 2001. Sheep are related to old traditional extensive agriculture; they were grazed in natural meadows, floodplains and wooded meadows of River Pedja, which are the most valuable habitats for many species and which are now overgrowing and disappearing.

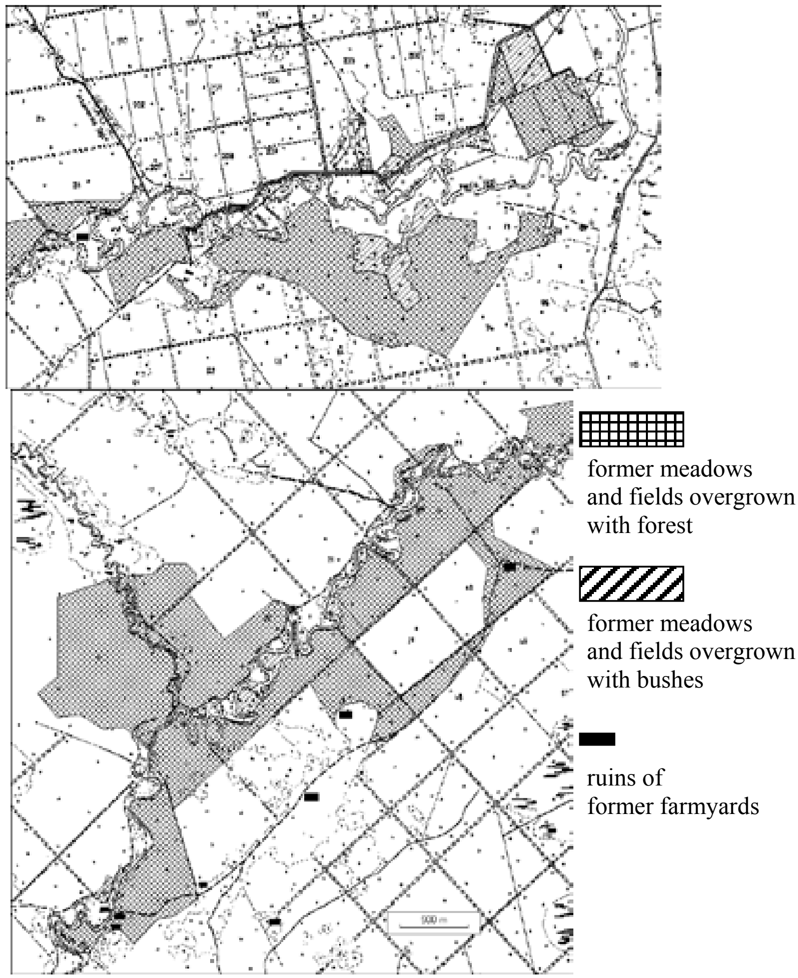

Figure 2: Land use changes in floodplains of River Pedja since 1936 (according to land cadastral map) to about 1990 (present cadastral map).

These changes are expressed in Figure 2. The area has also undergone such large-scale changes because between 1952 and 1991 it belonged to the Red Army and was entirely closed to all the public. Therefore, many people moved away from the area, farms were set aside, and now only ruins remain of the former farmsteads. All together in the territory of the Puurmanni Community, on the floodplains of the River Pedja, 547.2 ha of former meadows and flooded meadows are now overgrown; 514 ha have been replaced by forests and 33.2 ha by dense bushes.

4 Conclusions

During a short period, serious socio-economic changes took place in Estonia; these have certainly also had consequences for ecosystems and their ecological value. In the whole country, the share of agriculture in the GDP is steadily decreasing; agricultural production is decreasing and has resulted in the loss of jobs and the migration of people away from rural areas. Even a rural municipality with good physico-geographical conditions, such as fertile soils and proximity to cities, has suffered a decrease in agricultural production and in the number of animals and has witnessed the abandonment of agricultural areas. This has resulted in the loss of very valuable communities – wooded meadows and flooded meadows, which will have a direct impact on the diversity of plant and insect species in the area.

Acknowledgments

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AND POSSIBLE RELATION OF ACUTE PHASE PROTEINS WITH
SUBSEQUENT FERTILITY IN DAIRY COWS
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