National Oak Gall Wasp Survey – mapping with parabiologists in Finland

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1. Introduction

1.1. Parabiologists in data collecting

A parabiologist is an assistant in biological research without formal academic training. In the literature, these assistants are typically referred to as parataxonomists, as they are most often trained to collect, prepare and sort biological specimens for taxonomical purposes (Basset *et al.* 2004). Nevertheless, the term parabiologist can be used to describe people assisting other kinds of biological research, such as ecological or ethological studies (Lievonen 2001).

The main advantage of using parabiologists is cost-effectiveness. Because parabiologists are cheaper and potentially far more numerous than professional biologists, it makes sense to use them for some of the many tasks that professional biologists commonly perform, but which in fact will require no formal training. Parabiologists do not replace the professionals, but allow them to make better use of their time and expertise. The most common and cost-effective uses of parabiologists are in biodiversity assessment in the tropics and other labour intensive data collection (Basset *et al.* 2000, 2004). In Finland, untrained volunteers have been used before in sampling dung beetles (Roslin 2001).

Though biodiversity in the temperate zone is not on the same scale as in the tropics, parabiological methods are especially useful in assessing invertebrate faunas, and could be used to produce data for better-informed conservation planning (Goldstein 2004). This is of particular interest as the next round of the Evaluation of Threatened Species in Finland report is currently underway, and evaluators struggle with the too-common problem of insufficient distribution and abundance data for many species (Rassi *et al.* 2001).

Not all taxa are equally suited to parabiological methods. Ideally, the taxon should be one that can be sampled in a simple and easily standardised way. When the parabiologists are untrained and unpaid, as in this survey, there are further requirements: the study species have to have what it takes to make them both interesting to lay people and sufficiently easy for inexperienced observers to find and identify.

1.2. Oak cynipid gall wasps

The oak cynipid gall wasps of the tribe Cynipini lend themselves very well to parabiological sampling methods. These species have only one host plant in Finland, the pedunculate oak *Quercus robur*, which is sufficiently rare (Hämet-Ahti *et al.* 1998, Jalas & Suominen 1976) and well liked for people to take an interest in it. The galls of cynipids are easy enough to find - and in some cases even highly decorative. They can also be identified to the level of individual species and different generations within species. The larvae survive the removal of the gall from tree as well as transport by mail, and can then be reared to obtain the adults. Parabiological sampling was also a practical necessity for this study. Galls have to be collected within such a narrow time frame, especially in the case of the catkin galls, that a nationwide sampling could not be conducted by a single person.

Oak cynipid gall wasps are small specialist herbivorous insects on various species of Fagaceae, most often oaks (Hayward & Stone 2005, Redfern & Askew 1992). The tribe Cynipini belongs to the subfamily Cynipinae (Hymenoptera). This subfamily also includes four other tribes of specialist herbivores, and one tribe of species that live commensally as inquilines in the galls of other gall wasps (Nieves-Aldrey 2001). Female oak cynipids lay their eggs in their preferred part of the host plant using their long, sharp ovipositors. Oviposition induces the host plant to develop a gall around the egg, and as the larva develops, it feeds on the gall's specialised nutritive tissue. The larva goes through its entire development within the gall and emerges from it as an adult. The majority of oak cynipid species have two generations in a year, where one reproduces sexually (referred to as the sexual generation) and the other is composed entirely of females that reproduce by parthenogenesis (referred to in this text as the asexual generation) (Stone *et al.* 2002). Of all the tribes of gall wasps, the Cynipini is by far the most species-rich with about a thousand species in 27 genera (Hayward & Stone 2005). These numbers are changing constantly, firstly because the cyclically parthenogenetic life cycles of the Cynipini have often led to species being described twice and resolving them takes some effort, and secondly, because more species continue to be discovered, particularly in Central America, China and Southeast Asia (Csóka et al 2005).

The centre of oak cynipid species richness is in North America, particularly in Mexico: the Nearctic region has at least 700 species (Csóka et al 2005).

The oak cynipid's world distribution covers most of the Northern hemisphere, but the number of species declines east of the Pacific: the entire Palearctic region has some 200 species. The Western Palearctic has fewer species (circa 140) than the state of California alone (Csóka et al 2005), and only some 50 species are known from the Eastern Palearctic and Asia combined (Stone *et al.* 2002).

1.3. Motivations and objectives

In Finland, oak cynipids are interesting study organisms for spatial ecology. Because of the rarity and patchy distribution of the host plant, oak specialists live in a naturally fragmented landscape. From their point of view, individuals and groups of oaks will form patches of suitable habitat surrounded by unsuitable landscape. The persistence of oak cynipid species in a region may then depend not only on the presence but also the density and spatial configuration of the oaks (Hanski 1999): each local population of a gall wasp species may have a relatively short life span, due to population fluctuations or stochastic events. Therefore oak cynipids may depend on metapopulation processes (*sensu* Hanski & Kuussaari 1995) for persisting on a regional level. Thus the presence of oak specialist insects on a particular tree is likely to be influenced by how well it is connected to other oaks (for similar inferences on a leaf-miner, see Gripenberg and Roslin 2005).

In addition, Finnish gall wasps offer scope for questions of another type. In Finland, the host plant (*Q. robur*) reaches its northern distribution limit. The natural distribution of the pedunculate oak is limited to a narrow area on the south coast, but oaks have been planted north of it (Hämet-Ahti *et al.* 1998). This gives us an opportunity to examine how the incidence of individual oak cynipid species changes towards the edge of host's range, and how this is reflected in patterns on the level of the whole oak cynipid community.

The aim of this survey is to produce an updated list of the oak cynipid gall wasp species present in Finland, and to map their national distribution and local abundances. No such systematic survey has been made in this country before. I will also examine factors with a potential effect on the local incidence, species richness and abundance of oak cynipids - specifically, the isolation, geographic location, and size of the host tree. Finally, given the complex life cycles of oak cynipids, I will look at

whether the two generations of a species typically occur on the same individual trees, or whether a spatial shift in distribution between the two generations can be detected.

2. Material and Methods

This survey was conducted in 2007, the work beginning in January with the recruitment of volunteers. In order to cover both spring and autumn generations, we sampled in two periods, first in May/June and then in September.

2.1. The volunteers

The samples were collected by volunteers all over Finland. To concentrate my recruitment efforts on the people who would most likely be interested in the project, I advertised the study through the publications, websites, mailing lists and meetings of various organizations for Finnish nature lovers' organizations, using their publications, websites, mailing lists and meetings. I also contacted biology teachers and recruited colleagues, friends and family.

Central to recruiting volunteers was creating a website to which potential volunteers were directed by the advertisements (http://www.helsinki.fi/science/metapop/tammi/). On the website I posted a recruitment message, a sign-up form, general information about oak cynipids, sampling instructions and descriptions and pictures of all the known oak cynipid species in Finland. To maintain public interest in the project, I kept the website up to date throughout the study, with information on where I already had volunteers, when to start sampling, and how the study was progressing. I wrote the material together with my supervisors Tomas Roslin and Riikka Kaartinen and Sami Ojanen created the website itself (including the graphic design).

The volunteers who signed up over the internet were asked to fill out a form (Appendix 1) that recorded their contact information, the number of trees they intended to survey, their age group (under 15 / 15-25 / 26-65 / over 65), interests (plants / insects / birds / general nature / professional biologist) and duration of interest (less

than a year / some years / more than 10 years). This information was collected in order to provide guidelines for any similar projects in the future.

In order to remove any costs or unnecessary effort to the volunteers, and to standardise the sampling process, I sent every volunteer a package containing collecting materials for both spring and autumn surveys. Each package contained plastic bags, labels, addressed mailing boxes with the postage paid, tree information forms and sampling instructions.

2.2. Sampling

I instructed volunteers to conduct the spring sampling at the end of May and in the beginning of June, according to the individual phenology (timing of budbreak etc.) of the trees. Most of the volunteers received the additional message that sampling should ideally be done when the catkins are visibly releasing pollen. In the autumn round, I asked the volunteers to sample during the first half of September.

In deciding on the number of branches to sample from each tree, I tried to strike a balance between getting a representative sample and keeping the amount of work to a level that could be reasonably expected from unpaid volunteers. As a result, I asked the volunteers to designate a sampling area of five branch tips, each approximately half a metre long. To spread the sampling effort across different parts of the tree, the volunteers were asked to choose the branches evenly around the tree where possible. Nevertheless, as all the sampled branches had to be low enough to reach without tools, they were sometimes necessarily clustered together. The volunteers did not mark the branches in the spring, and the sampling area was designated anew in the autumn.

In the spring, I asked the volunteers to collect all the catkins in the sampling area, because catkin galls tend to be very difficult to find. After removing the catkins, the volunteers were asked to check both sides of all the leaves as well as the buds and the branch, to collect the entire leaf in the case of leaf galls, and to carefully remove the bud and twig galls from the branch. Apart from the catkins, the procedure was the same in the spring and in the autumn.

The volunteers were asked to put the material they had collected from each branch in its own bag, together with a label numbered from one to five. After

going through the sampling area, each volunteer spent an additional ten minutes freely examining the rest of the tree. They collected any galls found during these ten minutes into a sixth bag, together with a label marked “Extra”.

To obtain data on the location and characteristics of each tree, I asked the volunteers to fill out an information form (Appendix 2). This form recorded the sampler’s name, the date of sampling, the location of the tree (nearest population centre / coordinates if available), an approximation of the number of other oaks visible from the tree (1-5 / 6-10 / more than 10), habitat surrounding the tree (forest / open ground / forest edge / other), estimated tree height (under 2 m / 2-5 m / 5-10 m / over 10 m), trunk circumference at chest height (thinner than your wrist [under 16 cm] / between your wrist and your thigh [16-55 cm] / thicker than your thigh [>55 cm]), age of tree if known and origin of tree if known (wild or planted). In the autumn, the proportion of yellowed foliage was also estimated (less than one-fifth / between one-fifth and half / more than half). The volunteers also recorded various comments and observations. Finally, they placed the samples into a cardboard box in their separate bags and mailed them to me for processing.

2.3. Processing of samples

To monitor sample quality, I roughly graded the spring samples as to leaf size (reflecting phenological phase), presence or absence of catkins, presence or absence of pollen on the catkins, and occasional drying or decomposition in transit. I then went through the samples and identified and recorded the galls, and put all viable specimens into plastic vials to be reared in the context of another study (Riikka Kaartinen, in preparation). I recorded the galls separately for each branch. Identifications were based primarily on Redfern & Shirley (2002), and also Csóka (1997), Nieves-Aldrey (2001) and Redfern & Askew (1992).

In mapping the sampling locations, I used an internet service provided by the National Land Survey of Finland (http://kansalaisen.karttapaikka.fi/) and MapInfo Professional Version 8.5.

2.4. Data selection

For some of the sampled trees, factors that ruled out the occurrence of certain species, or which implied poor sample quality, became apparent on the tree information forms, or in my own grading of the arriving samples. I excluded these trees from statistical tests, but included positive findings on species-specific distribution maps (Table 1).

The problems that led to the exclusion of trees fell into two categories: problems of timing and problems of sampling technique. In the spring, I considered samples collected outside the period of May 24th to June 22nd to be collected at the wrong time, as after that period many spring galls begin to fall off the trees in southern Finland. In the cases of the sexual generations of the species *Andricus callidoma* and *Andricus glandulae*, whose galls develop exclusively on the catkins, I excluded samples from trees that had no catkins. Many of those trees had already ceased flowering at the time of sampling, as the spring of 2007 was unusually early (Finnish Meteorological Institute, http://www.fmi.fi/saa/tilastot_50.html#1).

Samples collected in the wrong way included trees where the correct sampling pattern of five branches and ten additional minutes was not followed. I also excluded some trees because of inadequate tree information, mainly vagueness in location information that would have made mapping unreliable. I further excluded some trees where the fallen leaves – and with them a lot of the overwintering galls – had been removed the previous autumn (Table 2).

For some species, I received additional observations from trees that were not examined systematically at all. These observations consisted of highly visible galls that the volunteers had noticed in passing and sent along with the regular samples. These additional observations are included in the distribution maps, but not in the statistical tests.

Table 1. Numbers of trees studied. Data from excluded trees were only used in distribution maps when the species was present. From distribution maps for exclusively catkin galling species, all the trees without catkins were excluded. Additional samples are observations from trees beyond those in the systematic survey.

Time period	Trees surveyed	Trees included in main survey	Included trees with catkins	Trees excluded	Additional samples
Spring	218	201	135	17	4
Autumn	180	178		2	10

Table 2. Reasons for exclusion from the main survey. "Wrong time" corresponds to trees sampled outside of the recommended period; "wrong sampling" to cases where the predefined sampling design had not been followed; "leaves removed" to trees from beneath which dead leaves had been removed in the autumn; and "insufficient information" to low accuracy in geographic information.

Reason	Trees excluded in spring	Trees excluded in autumn
Wrong time (too late)	3	
Wrong sampling	6	
Leaves removed	2	2
Insufficient information	6	
Total	17	2

2.5. Statistical analyses

To evaluate the adequacy of tree-specific sample sizes for detecting all the species present, I used species accumulation curves. I used the branch-level data (n=5 per tree plus the sample marked Extra; cf above) to graph the relative number of species found against the number of branches sampled. I did this for the fifteen trees from the spring sampling where four or more species were found.

To assess whether the different generations of the same species were to be found on different trees, I used Fisher's exact test on two by two tables of the numbers of trees occupied and unoccupied by the species in the spring and autumn. Separate tests were run for each of four species where both generations had been observed on at least ten trees sampled in both spring and autumn. For these tests I used SPSS Version 15.0.

To examine factors affecting overall species numbers as well as the incidence and abundance of individual species, I chose predictor variables describing the number of neighbouring oaks, tree circumference, latitude and longitude. To test for gradients running in other directions than straight north-south or east-west, I also included the interaction latitude×longitude. Of these variables, the number of neighbouring oaks and tree circumference had been scored on an ordinal scale, whereas latitude and longitude had been scored on a continuous scale.

To examine the effects of the five predictor variables on the local incidence of individual generations within species, I performed logistic regression analyses with the presence or absence of the species as the outcome variable. To examine the effects of the predictor variables on local species numbers and the local abundances of individual species, I used a generalised linear model, assuming a log link

and Poisson-distributed errors. Here, I included the species / generations that were present on at least twenty trees. In analysing the local abundance data, I only included the trees where the species was present (excluding all zeroes from the data). Statistical models were fitted with SAS Version 8.02 proc genmod.

The choice of predictor variables reflected not only *a priori* predictions, but also the actual quality of the data. Though requested from the volunteers, the data on the habitat, age and origin of each tree was too incomplete for statistical testing. Tree circumference and tree height (both reflecting tree size) were naturally highly correlated, and I chose tree circumference because it had been recorded for all the trees.

3. Results

3.1. Sampling success

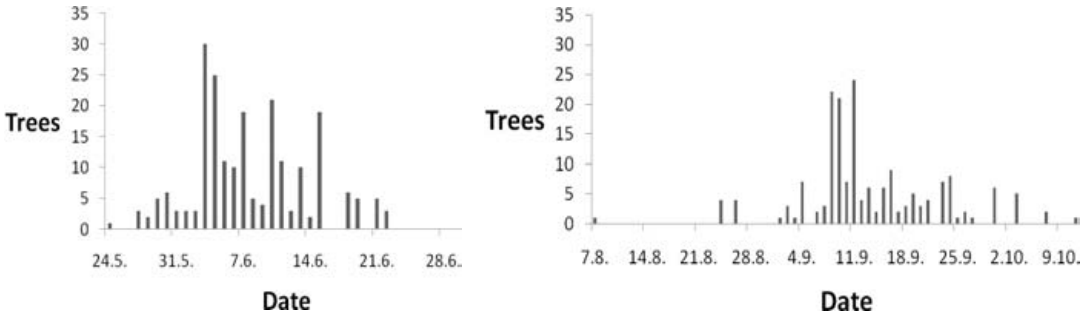
Overall, sampling success was high. Altogether 124 people signed up to sample 413 trees, but of the original volunteers, a significant proportion did not return samples or sampled fewer trees than they had originally planned. In the end, samples were taken from 218 trees in the spring and 180 trees in the autumn (Table 3). The majority of the trees were sampled within the suggested time windows of May-June and September (Figure 1).

More than one tree was sampled at most locations (Figure 2). Each volunteer sampled an average of 3.0 trees in the spring and 2.6 trees in the autumn, but the range was great: the busiest volunteer sampled 25 trees for both surveys, whereas 23 people in the spring and 20 in the autumn sampled a single tree.

Most of the volunteers who filled out the internet form gave the requested information about their age and background. All the age groups and interests suggested on the form were represented, but the majority of the volunteers were between twenty-six and sixty-five years old and took a general interest in nature (Figure 3).

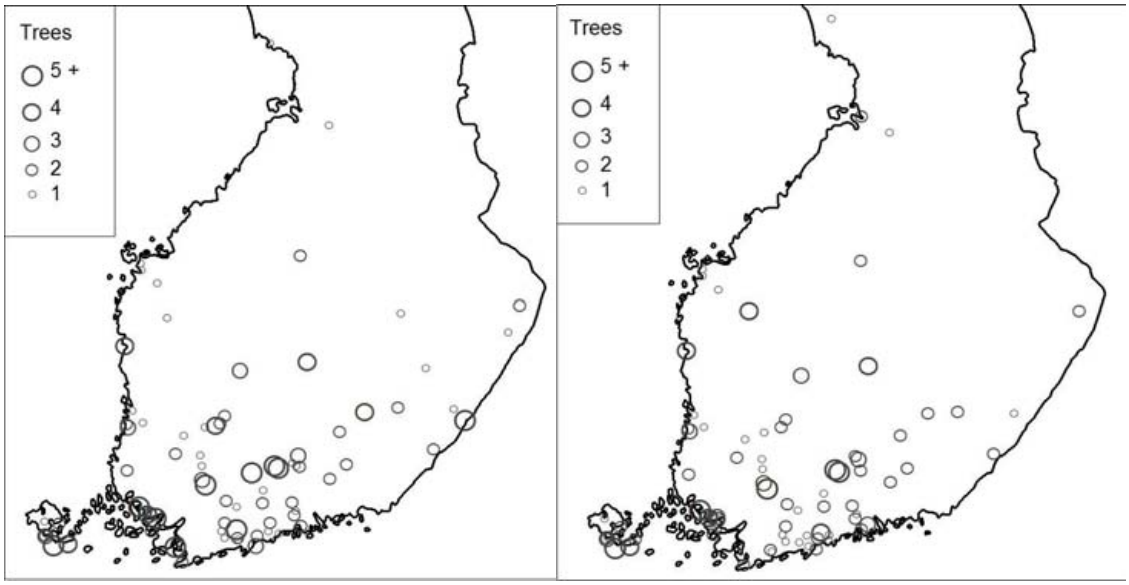
Table 3. Recruitment success and rates of sample return.

	No. of people volunteered	**No. of trees planned to be sampled**	**No. of people returning samples**	**No. of trees actually sampled**
Spring	114	381	72 (63%)	218 (57%)
Autumn	124	413	68 (55%)	180 (44%)



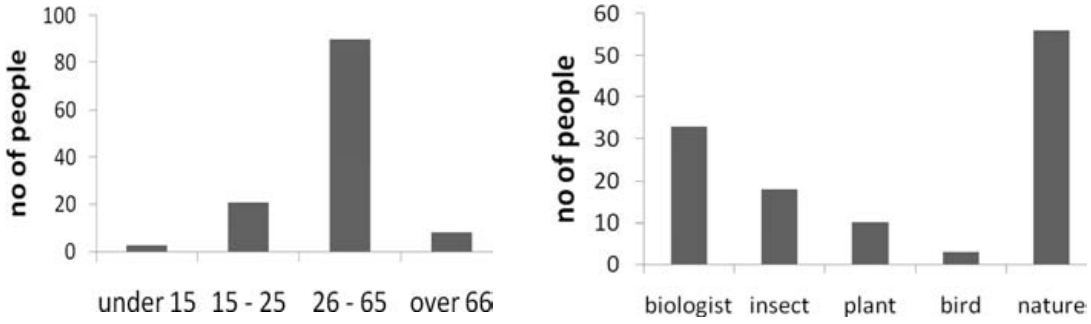
Spring (+2 trees 2.8.) Autumn

Figure 1. Frequency distributions of the sampling dates in the spring and autumn surveys. Two very late trees sampled for the spring survey on August 2nd were left out of the diagram.



Spring Autumn

Figure 2. Number of trees sampled per volunteer. Each circle represents a single volunteer at a single location. The size of the circle represents the number of trees sampled by the volunteer (see legend).



Age groups Interests

Figure 3. Frequency distributions of age groups (left) and main interests of volunteers (right) participating in the cynipid survey. Among interest groups, “biologist” identifies a volunteer with an academic training in biology, whereas “insect”, “plant” and “bird” identify amateurs interested in a specific taxon. “Nature” refers to an amateur with a general interest in nature.

Species accumulation curves revealed that the sample size was slightly lower than needed to capture the full complement of species present (Figure 4). While the curves did show a tendency to level out with more branches sampled, an additional ten-minute scan of the tree revealed new species in 23 % of the cases (Figure 4).

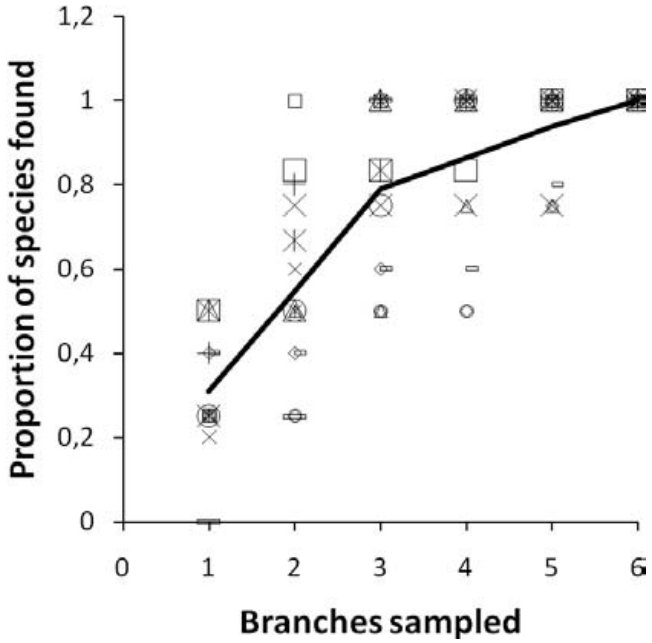


Figure 4. Species accumulation curves for fifteen trees (represented by different symbols) with four or more species found in the spring. The number of species detected in a given-sized sample is expressed as a proportion of the final number of species detected on the tree. "Branch 6" refers to a ten-minute scan of the foliage as performed after the five branches had been sampled. The line shows the average across trees.

3.2. The oak cynipid gall wasp fauna of Finland

This survey produced data on 16 species of oak cynipid gall wasps. Two of the species, *Andricus seminationis* and *Andricus testaceipes*, had not been found in Finland before. When combined with previous records (Riikka Kaartinen, Martti Koponen and Hans Silfverberg [Finnish Museum of Natural History], personal communications), the updated list of oak cynipid species recorded in Finland contains 21 species (Table 4). In addition to the confirmed species identifications, I also found possible examples of the species *Andricus corruptix, Andricus kollari*, *Andricus quercuscorticis* and *Neuroterus albipes*. Unfortunately I have been unable to verify these tentative identifications. One species, of which I found six galls, is still to be identified.

Table 4. An updated checklist of oak cynipid species recorded in Finland. "No. galls found in spring" and "No. galls found in autumn" refer to the total numbers of galls observed during the spring and autumn sampling, respectively. "Trees where present in spring" and "Trees where present in autumn" identify the number of trees on which the species was detected during the sampling round (out of 218 and 180 trees sampled in spring and autumn, respectively)[1]. The last column identifies references for previous findings of the species in Finland[2].

Species	Gene-ration	Galls found in spring	Trees where present in spring	Galls found in autumn	Trees where present in autumn	Found previ-ously
Andricus callidoma	sexual	814	41	18	1	HS
Andricus callidoma	asexual	2	1	18	10	HS
Andricus curvator	sexual	1009	34	325	26	HS
Andricus curvator	asexual	0	0	0	0	HS
Andricus foecundatrix	sexual	0	0	0	0	HS
Andricus foecundatrix	asexual	16	4	87	14	HS
Andricus glandulae	sexual	754	40	0	0	RK
Andricus glandulae	asexual	0	0	0	0	RK
Andricus nudus	sexual	0	0	0	0	RK
Andricus nudus	asexual	0	0	10	4	RK
Andricus paradoxus	sexual	0	0	0	0	RK
Andricus paradoxus	asexual	0	0	1	1	RK
Andricus pseudoinflator	sexual	277	31	141	25	HS
Andricus pseudoinflator	asexual	0	0	223	26	HS
Andricus quadrilineatus	asexual	2509	94	21	6	HS
Andricus quercusradicis	both	0	0	0	0	HS
Andricus quercusramuli	sexual	41	9	37	6	HS
Andricus quercusramuli	asexual	0	0	0	0	HS
Andricus seminationis	asexual	36	3	3	1	
Andricus testaceipes	sexual	0	0	0	0	
Andricus testaceipes	asexual	1	1	0	0	
Cynips disticha	both	0	0	0	0	MK
Cynips divisa	sexual	107	10	1	1	HS
Cynips divisa	asexual	0	0	1011	22	HS
Cynips longiventris	sexual	0	0	0	0	HS
Cynips longiventris	asexual	0	0	128	30	HS
Cynips quercusfolii	both	0	0	0	0	HS
Neuroterus anthracinus	sexual	45	15	0	0	RK
Neuroterus anthracinus	asexual	10	2	1512	69	RK
Neuroterus numismalis	sexual	0	0	80	10	HS
Neuroterus numismalis	asexual	0	0	58	0	HS
Neuroterus quercusbaccarum	sexual	701	28	125	11	HS
Neuroterus quercusbaccarum	asexual	0	0	362	14	HS
Neuroterus tricolor	both	0	0	0	0	HS
(Biorhiza pallida)[3]	both	0	0	0	0	HS

[1] Additional samples (see 2.4., *Data selection*) are included in numbers of galls, but not in numbers of trees. For instance, all 58 galls of the asexual generation of *Neuroterus numismalis* relate to such an additional sample, whereas none were found on the 180 trees systematically sampled in the autumn.

[2] RK = Riikka Kaartinen, *personal communication*, MK = Martti Koponen, *personal communication*, HS = Hans Silfverberg (Finnish Museum of Natural History), *personal communication*.

[3] *Biorhiza pallida* occurs in brackets, since all previous observations of the species were made in areas now forming part of Russia.

The average number of species in a tree was 1.45 (SD= 1.40 in the spring sampling and 1.47 (SD= 1.45) in the autumn. In 33% of the trees no species were found, whereas a maximum of six species was recorded on 1% of trees (Figure 5). From a spatial perspective, species numbers tended to decline toward the northeast (Figure 6).

Tree size, isolation and geographic location all had a significant effect on local species numbers (Table 5). In the spring, a significant effect was detected for every factor examined (Table 5). Here, the bigger the tree and the more oaks that were visible from it, the more species were found (Figure 7), as evident against a backdrop of general clines in species richness with latitude and longitude (Table 5). In the autumn, only geographic location had any detectable effect on local species richness (Table 5).

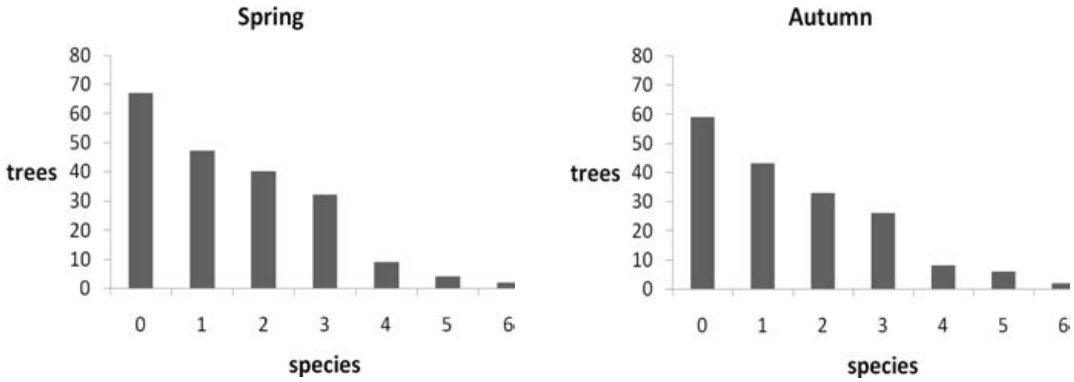


Figure 5. Number of gall wasp species found on individual trees during spring and autumn.

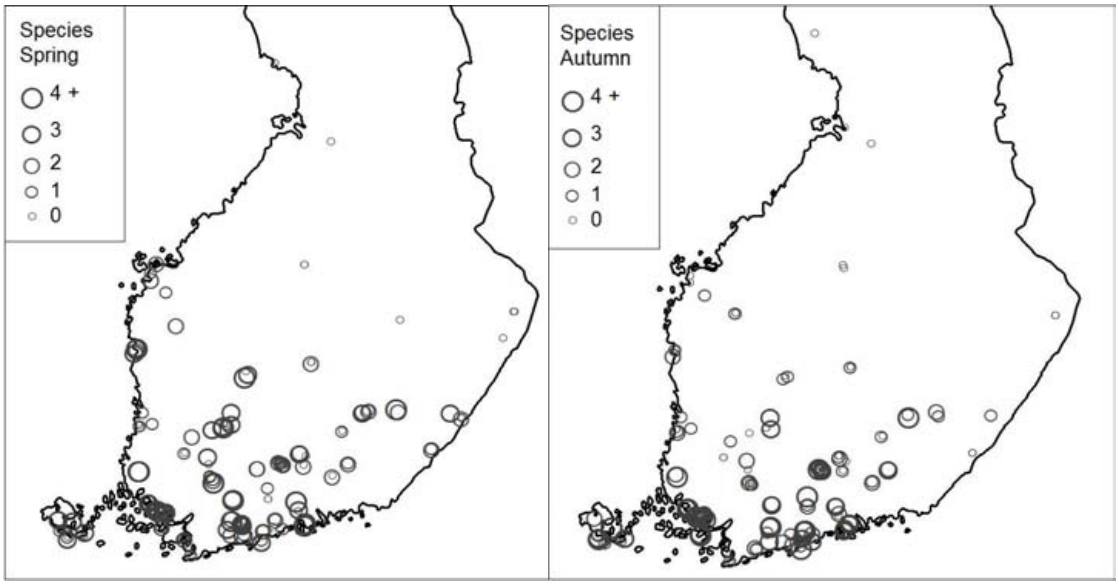


Figure 6. Numbers of species detected on individual oak trees during the spring and autumn samplings.

Table 5. Generalized linear models of factors affecting species numbers during the spring and autumn. The outcome variable is the number of species, predictor variables are number of neighbouring oaks (categorical variable), tree circumference (categorical variable), latitude (unit 50 km) and longitude (unit 50 km). To pinpoint significant results, asterisks in column "Sig. class" identify test results for which P<0.05 (*); P< 0.01 (**) ; and P<0.0001 (***).

Sampling	Factor	DF	χ^2	P	Sig. class
Spring	Neighbouring oaks	3	12.52	0.0058	**
	Circumference	2	27.40	<.0001	***
	Latitude	1	15.04	0.0001	***
	Longitude	1	15.58	<.0001	***
	Lat. × lon.	1	15.61	<.0001	***
Autumn	Neighbouring oaks	3	4.41	0.22	
	Circumference	2	2.37	0.31	
	Latitude	1	3.43	0.064	
	Longitude	1	4.36	0.037	*
	Lat. × lon.	1	4.33	0.038	*

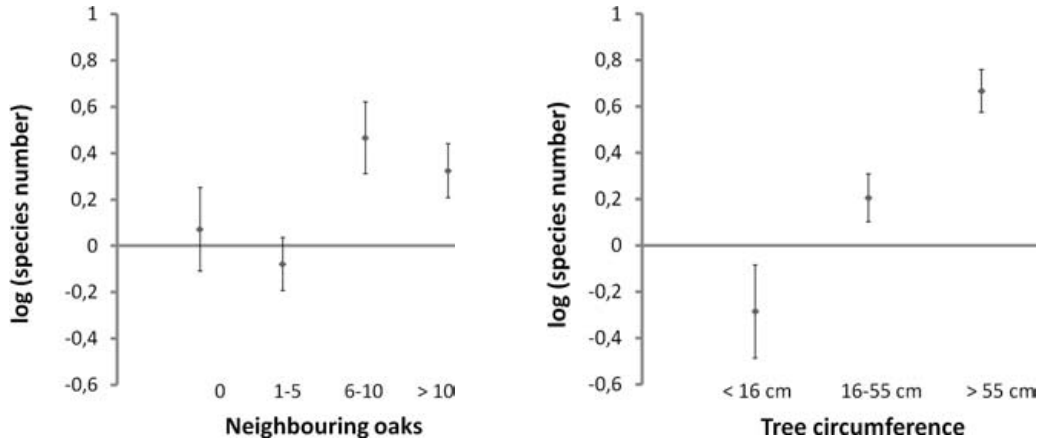


Figure 7. Least squares means (with standard errors) for the effect of the number of neighbouring oaks (left) and tree circumference (right) on local species richness in the spring data.

3.3. Factors affecting the distributions of individual species

Of the four species examined, the asexual and sexual generations were to be found on different trees more often than expected by chance alone in three species (Table 6). This indicates that the distribution of different generations may be affected by different factors, and I therefore modelled the distribution of each species and generation separately.

Table 6. Fisher's exact tests of species incidence on individual trees in the spring and autumn generations. Included are four species where both generations had been observed on at least ten trees sampled in both spring and autumn.

Species	Fisher's exact P
Andricus callidoma	0.21
Andricus pseudoinflator	0.001
Cynips divisa	0.014
Neuroterus quercusbaccarum	0.0001

Patterns observed at the level of general species richness (section 3.2.) were also reflected in the distribution patterns of individual species and generations: the local incidence of some of the species was significantly influenced by the number of neighbouring trees, by tree circumference, latitude and longitude (Table 7). Of fifty tests, statistically significant effects ($P < 0.05$) were found in thirteen (26 %), which is a higher fraction than what would be expected from chance alone (5 %; Table 7).

In three cases, I found evidence of large-scale clines in distribution, as species-specific incidence was affected by latitude, longitude and/or their interaction. These cases concerned the sexual generation of *Andricus glandulae* and the asexual generations of *Andricus quadrilineatus* and *Cynips longiventris*. In the sexual generations of *Andricus curvator* and *Neuroterus quercusbaccarum*, incidence was significantly higher on trees with more neighbouring oaks. In the sexual generation of *Andricus callidoma* and the asexual *Andricus quadrilineatus*, incidence was significantly higher on trees with a greater circumference.

In contrast to the patterns found for the species' incidence, the local abundances were not detectably affected by the factors examined here. Of eighty tests applied to the same ten species / generations as examined in terms of incidence, I found statistically significant effects in only five (6%), and these effects were related to different factors. Since such patterns can be ascribed to chance alone, I conclude that the local abundances of species are influenced by factors beyond the present analysis.

Table 7. Logistic regression models for factors affecting the incidence of ten individual cynipid species / generations. The outcome variable was presence of the species, the predictor variables were the number of neighbouring trees, tree circumference, latitude and longitude. To faciltate the pinpointing of significant results, asterisks in column "Sig. class" identify test results for which P<0.05 (*); P< 0.01 (**) ; and P<0.0001 (***).

Species	Generation	Factor	DF	χ^2	P	Sig. class
Andricus callidoma	sexual	Neighbours	3	3.76	0.29	
		Circumference	2	11.68	0.003	**
		Latitude	1	0.83	0.06	
		Longitude	1	0.87	0.06	
		Lat. × lon.	1	0.91	0.06	
Andricus curvator	sexual	Neighbours	3	10.90	0.01	*
		Circumference	2	4.87	0.09	

		Latitude	1	2.91	0.09	
		Longitude	1	3.09	0.08	
		Lat. × lon.	1	3.08	0.08	
Andricus glandulae	sexual	Neighbours	3	5.75	0.12	
		Circumference	2	2.38	0.30	
		Latitude	1	8.50	0.004	**
		Longitude	1	8.20	0.004	**
		Lat. × lon.	1	8.32	0.004	**
Andricus pseudoinflator	sexual	Neighbours	3	1.44	0.70	
		Circumference	2	4.43	0.11	
		Latitude	1	0.13	0.72	
		Longitude	1	0.08	0.78	
		Lat. × lon.	1	0.08	0.77	
Andricus pseudoinflator	asexual	Neighbours	3	0.71	0.87	
		Circumference	2	0.24	0.89	
		Latitude	1	0.29	0.59	
		Longitude	1	0.28	0.60	
		Lat. × lon.	1	0.29	0.59	
Andricus quadrilineatus	asexual	Neighbours	3	4.55	0.21	
		Circumference	2	10.74	0.005	**
		Latitude	1	4.73	0.03	*
		Longitude	1	4.96	0.03	*
		Lat. × lon.	1	4.91	0.03	*
Cynips divisa	asexual	Neighbours	3	0.31	0.96	
		Circumference	2	2.20	0.33	
		Latitude	1	2.63	0.10	
		Longitude	1	2.91	0.09	
		Lat. × lon.	1	2.82	0.09	
Cynips longiventris	asexual	Neighbours	3	3.02	0.39	
		Circumference	2	0.78	0.68	
		Latitude	1	4.57	0.03	*
		Longitude	1	5.23	0.02	*
		Lat. × lon.	1	5.10	0.02	*
Neuroterus anthracinus	asexual	Neighbours	3	6.52	0.09	
		Circumference	2	1.08	0.58	
		Latitude	1	0.79	0.37	
		Longitude	1	1.04	0.31	
		Lat. × lon.	1	1.03	0.31	
Neuroterus quercusbaccarum	sexual	Neighbours	3	11.92	0.008	**
		Circumference	2	0.57	0.75	
		Latitude	1	0.01	0.91	
		Longitude	1	0.01	0.91	
		Lat. × lon.	1	0.01	0.92	

3.4. Species-specific patterns

A main objective for this study was to provide the first descriptions of species-specific distribution patterns within Finland. In interpreting species-specific distribution patterns, the relative detectability of each species and generation has to be taken into account. I will next describe the general distribution patterns as revealed by my sampling, and comment on factors with a potential bearing on detectability.

Andricus callidoma (Hartig, 1841): Widespread throughout southern Finland and Åland (Figure 8 A). The sexual generation galls develop on catkins and are

abundant but very hard to find without experience. (In the current study, I inspected all the catkins on the sampled branches myself, thus standardising the probability of detection.) The asexual generation galls are uncommon but easily found.

Andricus curvator (Hartig, 1840): Widespread throughout southern Finland and Åland (Figure 8 B). The sexual generation of this species is abundant and easy to find on the leaves, and the empty galls persist for as long as the leaf remains attached. For this reason sexual generation galls were found in both spring and autumn surveys. Asexual generation galls are hard to find, and indeed none were found.

Andricus foecundatrix (Hartig, 1840): Distributed along the southern coastline and inland in the southeast (Figure 8 C). No sexual generation galls were found; they develop on catkins but are hard to find. The asexual generation galls are quite common and highly visible and the empty galls can persist for several years, so old galls were found in both spring and autumn.

Andricus glandulae (Hartig, 1840): Widespread throughout southern Finland, and also found on Åland (Figure 8 D). The sexual generation galls are abundant and develop on the catkins. The asexual generation galls are not hard to find, but none were detected in this survey.

Andricus nudus (Adler, 1881): Only a few observations in the south and in Ostrobothnia (Figure 8 E). No sexual generation galls were found in this survey, even though they develop on the catkins. The asexual generation galls are quite visible, but not many were found.

Andricus paradoxus (Schlechtendal, 1870): Only one observation in this survey, in southern Finland (Figure 8 F). The sexual generation galls develop on catkins and are very difficult to find, even for an experienced seeker. The asexual generation galls are easy to find, and the one example of this species found in this study was an asexual generation gall.

Andricus pseudoinflator (Hartig, 1840): Widespread and abundant throughout southern Finland and also found in Åland (Figure 8 G). The galls of both generations are easily found.

Andricus quadrilineatus (Hartig, 1840): Both the most widespread and the most abundant species in this survey, with frequent records throughout southern Finland and Åland (Figure 8 H). The asexual generation galls develop on catkins and leaves and are relatively easy to find. No sexual generation is known for this species.

Andricus quercusramuli (Linnaeus 1761): Found on the southwestern and southern coasts and on Åland (Figure 8 I). The sexual generation galls are highly visible and quite common, the asexual generation very hard to find. No asexual generation galls were found, but some old sexual generation galls were recorded in the autumn.

Andricus seminationis (Giraud, 1859): One of two species new to Finland found in this survey, with a few records made throughout southern Finland (Figure 8 J). No sexual generation is known, and the asexual generation gall is easy to find. Where present, the asexual generation gall is quite common.

Andricus testaceipes (Hartig, 1840): A new species to Finland, with only one specimen found on the southwest coast (8 K). The galls of both generations are hard to find; the sexual generation galls develop in the leaf blades, the asexual generation galls under the bark. The one example that was found was an old, emerged cluster of asexual generation galls.

Cynips divisa (Hartig, 1840): Relatively widespread in southern Finland, with a range extending from the middle of Southern Finland to the south coast (Figure 8 L). The galls of both generations are easy to find: the sexual generation galls are quite common and the asexual generation abundant

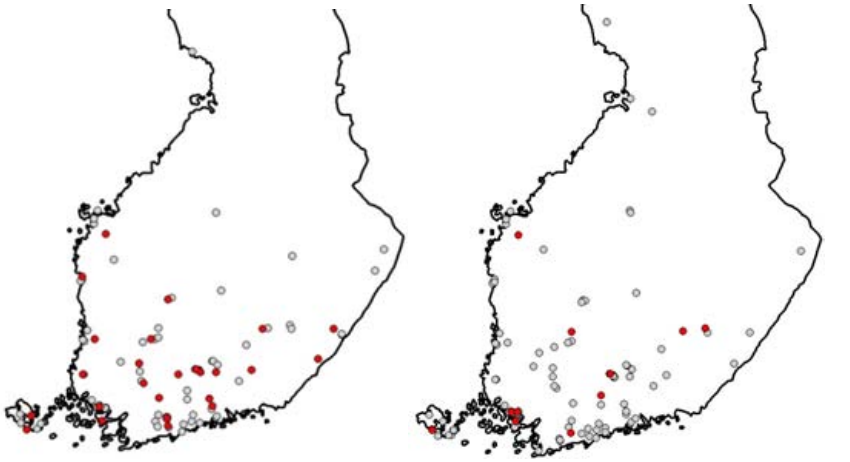
Cynips longiventris (Hartig, 1840): Widespread in southern Finland, and also found on Åland. On the mainland, it occurred in the southwest and the southeast (Figure 8 M). The sexual generation galls are difficult to find, and none were detected in this survey. The asexual generation galls are highly visible and quite common.

Neuroterus anthracinus (Curtis, 1838): Widespread in southern Finland, particularly on the south coast and on Åland (Figure 8 N). The sexual generation galls are uncommon and quite hard to find, whereas the asexual generation galls are easily detected and abundant.

Neuroterus numismalis (Geoffroy, 1785): Found at only a few locations on the south coast and Åland (Figure 8 O). The galls of both generations are easy to find and where found, they are quite common.

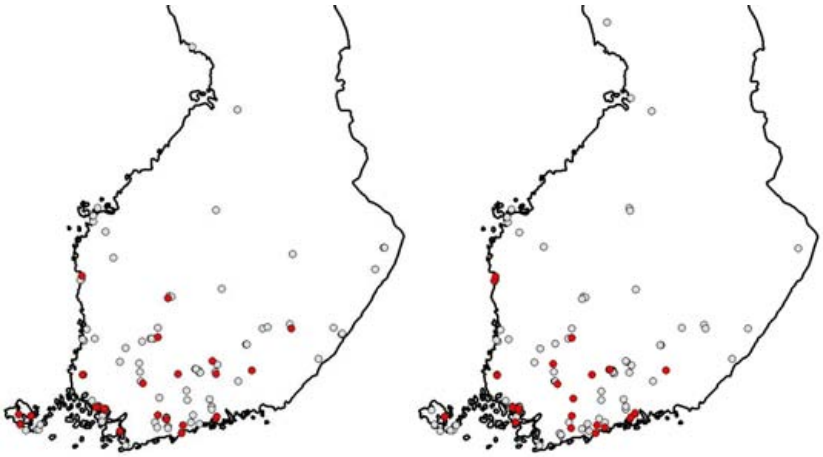
Neuroterus quercusbaccarum (Linnaeus, 1758): Widespread and abundant in southern Finland and on Åland. In this species, the two generations seem to have slightly different distributions. In the spring, the species was widespread throughout the southern part of the country (Figure 8 P). In the autumn, the distribution contracted to the southwest corner of the country, with an expansion southwest onto Åland. The galls of both generations are easy to find.

A) *Andricus callidoma*



Spring (sexual generation) Autumn (asexual generation)

B) *Andricus curvator*



Spring (sexual generation) Autumn (persisting sexual generation)

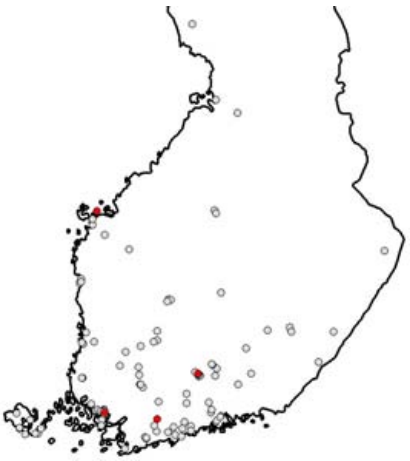
C) *Andricus foecundatrix*

D) *Andricus glandulae*



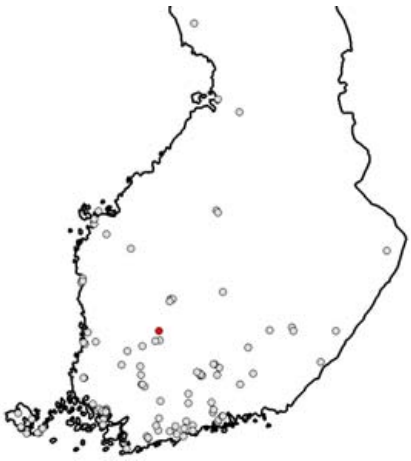
Autumn (asexual generation, live and old galls) Spring (sexual generation)

E) *Andricus nudus*



Autumn (asexual generation)

F) *Andricus paradoxus*

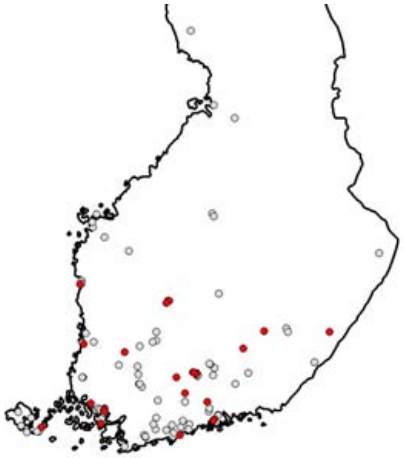


Autumn (asexual generation)

G) *Andricus pseudoinflator*

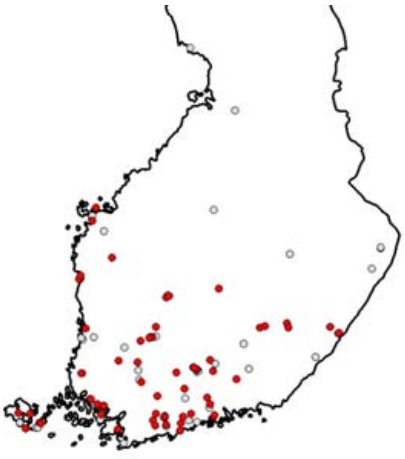


Spring (sexual generation)



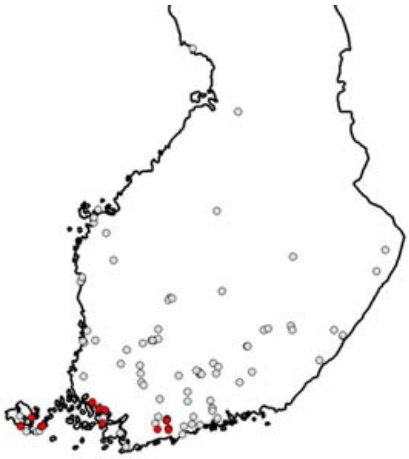
Autumn (asexual generation)

H) *Andricus quadrilineatus*



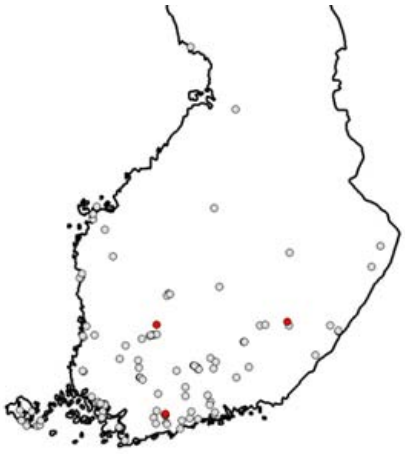
Spring (asexual generation)

I) *Andricus guercusramuli*



Spring (sexual generation)

J) *Andricus seminationis*



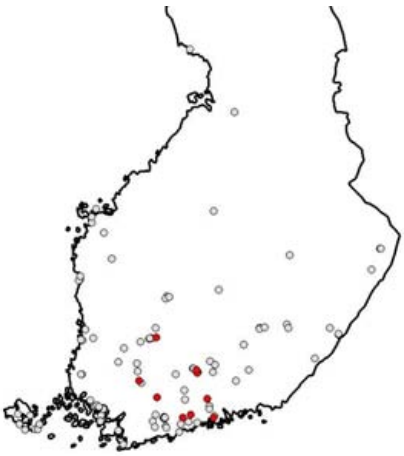
Spring (asexual generation)

K) *Andricus testaceipes*

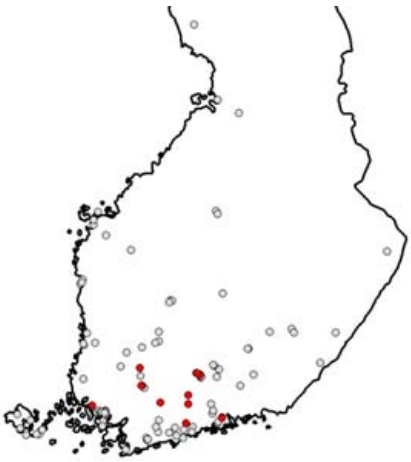


Spring (asexual generation)

L) *Cynips divisa*

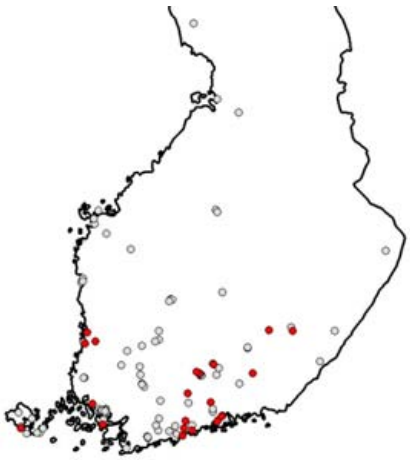


Spring (sexual generation)



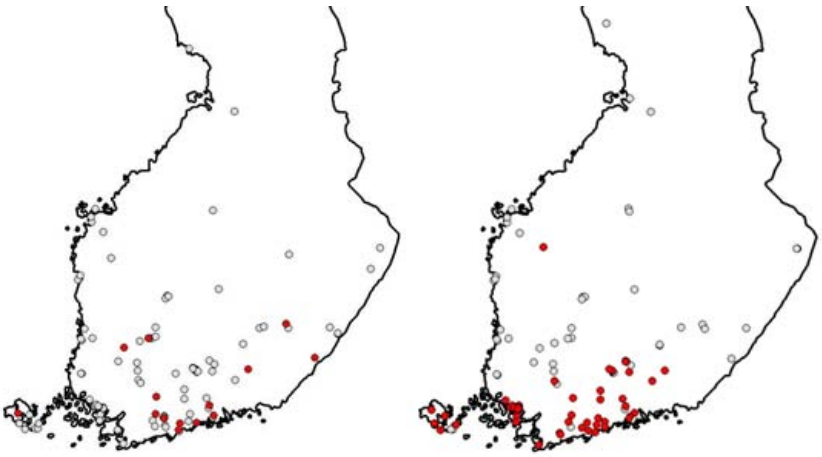
Autumn (asexual generation)

M) *Cynips longiventris*



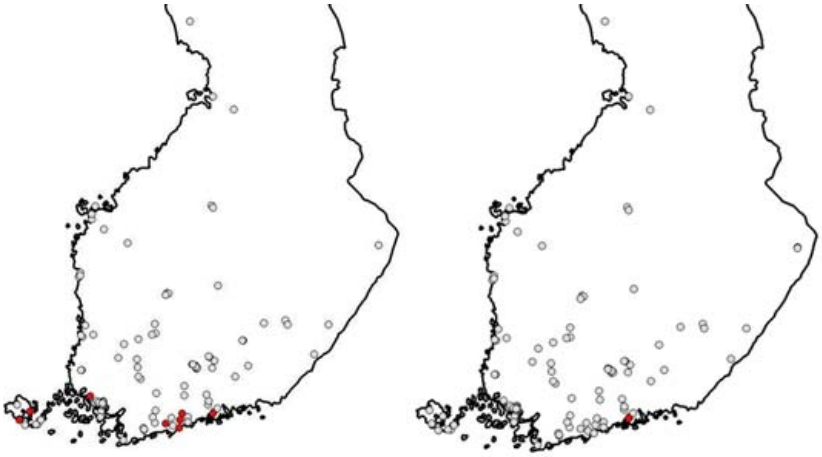
Autumn (asexual generation)

N) *Neuroterus anthracinus*



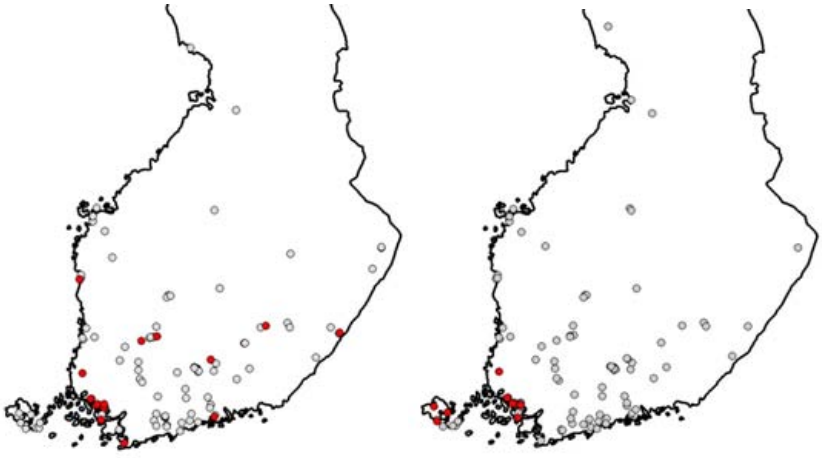
Spring (sexual generation) Autumn (asexual generation)

O) *Neuroteus numismalis*



Autumn (sexual generation) Autumn (asexual generation)

P) *Neuroterus quercusbaccarum*



Spring (sexual generation) Autumn (asexual generation)

Figure 8. Distribution maps for individual species and their different generations. Red points indicate trees where the species / generation was present, grey points trees where it was not.

4. Discussion

This survey demonstrates how parabiologists can successfully be used to reveal large-scale patterns in the distribution of a poorly known insect taxon. Based on the sampling effort of over a hundred volunteers, I was able to construct the first distribution maps for oak cynipids in Finland – a task that had not been achievable with professional biologists alone. The total sampling effort from the volunteers roughly corresponds to over half a person-year. Nevertheless, no single person (and no small group of persons) could have produced this effort within the time frame required. Since the galls, particularly the catkin galls, occur during a short period of time, a massive, simultaneous effort is necessary. But before examining the patterns revealed by this survey, I will assess the quality of data actually achieved.

4.1. Data quality

The quality of the data collected by volunteers will largely depend on the extent to which an untrained observer is able to detect the galls. There are two points here: the first being the sufficiency of the sampling effort per tree in getting a representative sample of a particular tree's oak cynipid fauna. Species accumulation curves suggest that my approach of sampling five branches per tree, as followed by a ten-minute scan of the foliage, was slightly lower than optimal. Although the resulting curves (Fig. 4) did show some signs of levelling off, many curves failed to reach an asymptote. However, increasing the sampling effort further would have increased the time the volunteers had to spend on each tree, which might in turn have decreased participation, sample return rates and accuracy. Furthermore, a study conducted in the United Kingdom suggests that a relatively low effort is indeed sufficient for detecting the cynipid species present in a tree. As reported by Leach and Mason (1999), a trained observer searching systematically need spend no more than five minutes per tree or 30 minutes per site in order to achieve a reliable estimate of the local cynipid assemblage. The observers in this study, though untrained, examined each tree systematically for about an hour. Moreover, they did not need to identify the species, but simply collect and send in anything that they thought might be a gall. In conclusion, increasing the local sampling effort might have produced a few more observations per tree, but

potentially at a substantial cost. I therefore conclude that the sampling effort was a successful compromise between different considerations, and that the samples obtained will offer decent estimates of local species assemblage and incidence. While lower-than-perfect detection probabilities may have introduced some noise in the material, this should not introduce any serious bias in the results.

The second point about the reliability of the sampling concerns variation in the detection of different galls. To quantify this error, I tested the effect of visibility by grading the galls of all the species ever found in Finland and their different generations (Table 4) as either visible or cryptic. As a basis for this classification, I used my own experience and that of Redfern & Shirley (2002). Based on a two-by-two table of the numbers of cryptic and visible galls that were found and not found, the likelihood of finding a given species / generation was indeed affected by its visibility (Fisher's Exact $P < 0.0001$). This does suggest that some cryptic generations have been missed in the sampling. Nevertheless, this effect will hardly extend as far as to entire species being missed, since of the five species that were previously known to Finland but not found in this survey, only one – *Andricus quercusradicis* – is cryptic in both generations. The other four species not detected in this study have at least one highly visible generation that should have been noticed if it was present in the study area. It is thus unlikely that entire species were missed because of the volunteer's lack of experience. Overall, I conclude that the present sampling will be adequate for contributing to the knowledge of the oak cynipid gall wasp fauna of Finland.

4.2. The oak cynipid gall wasp fauna of Finland

This survey suggests that Finland maintains a relatively rich fauna of oak cynipids. Although Finland has only one oak species, and that species reaches its northern distribution limit not far from the south coast, 21 species of oak cynipids have now been recorded from the region. To compare, some 35 species have been recorded from the United Kingdom (Leach and Mason 1999), and 27 species from Sweden (Martti Koponen, personal communication). In Finland, oak cynipids are also quite common as a group, as they were found in two thirds of the trees sampled for this study.

As could be expected, oak cynipids are most common and diverse in the southwest, where oak trees are numerous, and the natural old oak forests in that part of

the country are clearly important to this taxon. The wide distributions of some species such as *Andricus pseudoinflator*, however, are surprising: finding several species as far north as Ostrobothnia challenges the notion that oak cynipids are southern species. It would seem, then, that the distribution of oak cynipids is limited by factors other than those limiting the natural distribution of the host: cynipids have spread successfully beyond the natural distribution of *Quercus robur* and colonised the planted trees in the north.

Elsewhere in the world, there are other cases of oak cynipid distributions being widened by human activity. For example, *Quercus cerris*, originally inhabiting Italy, the Balkans and Asia Minor, has been widely planted north and west of its native range in the last 400 years. In that time, eight host-alternating species and two species thought to depend solely on *Q. cerris* have spread as far the United Kingdom (Csóka *et al* 2005, Stone *et al* 2001). A large complement of parasitoids and inquilines have spread along with these species, creating interesting patterns in local assemblage composition (Schönrogge *et al.* 1995, 1998, 2000, Schönrogge & Crawley 2000).

Within Finland, not all the cynipid species have spread equally far north, though: there are great differences in the size of the distribution area between the different species. For instance, in comparison with the aforementioned *Andricus pseudoinflator*, *Neuroterus anthracinus* is much more restricted to the south, even though it is much more abundant and was found on more trees. Abundance, too, varied greatly, from species that were represented by a single gall to the most common species *Andricus quadrilineatus*, which was found on 43% of the sampled trees. These differences between species create large differences in local gall wasp assemblages across Finland.

4.3. Factors affecting species numbers and incidence

As well as reporting large scale patterns in community structure, this study also reveals some of the factors affecting them. As oak cynipids inhabit a naturally fragmented landscape, the metacommunity concept offers a useful perspective here. A metacommunity consists of multiple interacting species occurring at several discrete sites that are linked by migration (Leibold *et al* 2004). Two major factors may potentially create variation in local species assemblage in a metacommunity context: the

spatial structure of the system and spatial heterogeneity in site quality (Leibold & Miller 2004, Tscharntke *et al.* 2002). In the context of the current study system, an effect of spatial structure would emerge if species responded to the relative connectivity of an oak, and an effect of site heterogeneity would result if different species preferred different kinds of oaks (cf. Abrahamson *et al.* 2003, Jeffries *et al.* 2006, Lawrence *et al.* 2003, Lawton 1983). As a measure of connectivity, I used the number of neighbouring oaks, and as a measure of patch quality, I used the size of the tree. While my results suggest that both factors play a role, both the measures themselves and the underlying assumptions deserve some scrutiny.

With the sampling method used here, it would have been impossible to get any of the conventional measures of connectivity, as they all require field measurements. My measure of connectivity resembles a "buffer measure", which takes into account the number of occupied patches within a certain radius from the focal patch (Moilanen & Nieminen 2002). As a key difference compared to traditional buffer measures, the connectivity measure I used takes into account all the potential habitat patches, regardless of whether or not they are occupied. Also, the radius of the buffer zone is quite vague, as it is influenced by the matrix habitat. In dense forest or in a built-up area it is shortened by limited visibility, whereas at open ground sites with high visibility it encompasses more oaks.

My measure of habitat quality is based on the assumption that oak trees undergo ontogenetic changes with increasing age, thereby changing in quality (Boege & Marquis 2005, Donaldsen *et al.* 2006, Laitinen *et al.* 2004). A tendency for the different generations to be found on different types of trees has been noted before for *Neuroterus quercusbaccarum* and *Neuroterus numismalis*, and has been attributed to differences in host phenology. In these species, the sexual generation is more often found on trees that open their leaves early, the asexual generation being found on trees with a late bud break (Askew 1962, Crawley & Akhteruzzaman 1988).

Despite the preliminary support for effects of both patch quality and spatial configuration, it should be noted that my measure of spatial location was partly confounded with the surrounding habitat, and my measure of tree quality partly confounded with many different factors. In a forest habitat, a high number of oaks would indicate that the tree is growing in an oak forest, whereas a low number of oaks may mean that the tree is growing in a coniferous forest. For this reason, the current results should not uncritically be seen as support for spatial effects alone. Regarding

tree quality, the current pattern could attributed to any one of several alternative explanations: a larger tree may sustain larger and more persistent local populations of cynipid wasps (e.g. Gripenberg *et al.* 2008), may provide more different kinds of resources, and be easier for a dispersing individual to find and colonise (Cornell 1986). Thus, this study has not fully disentangled the relative effects of habitat quality and spatial configuration. Nevertheless, it suggests a role for both, and points the way for interesting research in future.

4.4. Conclusions

The single most important outcome of this study is the demonstration that large-scale biological data can be obtained by the coordinated effort of untrained volunteers. Parabiological sampling could be used to produce data on other poorly known taxa, as oak cynipids are by no means the only specialist insects with a sessile and easily detected stage in their life cycles. This project has also increased public awareness of oak cynipids, and hopefully brought new enthusiasts to them. The observations of such enthusiasts could continue to be used in monitoring changes in Finland's oak cynipid species assemblages. To facilitate these long-term aims, I will continue to maintain the infrastructure and web-based material developed for this project, and advance the transfer of the data collected to museum databases.

5. Acknowledgements

I am extremely grateful to my supervisor Tomas Roslin for working so hard on this and for being endlessly patient and supportive. He commented extensively on more versions of this text than I can count, taught me to use the software and guided me through the statistical tests. My second supervisor Riikka Kaartinen also commented on several versions, taught me all about gall wasps, and always knew when I needed a drink. Tomas and Riikka suggested this idea in the first place, and we did all the planning together.

Sami Ojanen at the MRG created the website and was such a pro. Thanks to Ayco Tack for helpful discussions and references, and for being my other gall wasp

guru. Pretty much everyone in the Korppoo gang got roped into helping out at some point: thanks to all of them for being great company, too. Ivis was my spare brain who kept the mailing operation from sliding into chaos. Mum stayed serene when I took over the house and was always there in an emergency.

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Finally, thank you most of all to the volunteers who made this survey possible in the first place: I hope you enjoyed yourselves out there.

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Appendices

Appendix A: Sign-up form

Name:

Address:

Post code and area:

Email address:

Age: Less than 15 □ 15-26 □ 26-65 □ 66 or older □

How many trees do you plan to sample?

Main interest: Insects □ Plants □ Birds □ General nature □

Professional biologist □

Duration of interest: Less than a year □ Some years □ Over ten years □

Would you like to receive information about similar projects in the future? Yes □ No □

Appendix B: Tree information form

Tree information

Fill out a form for each tree.

Even if you don't find any galls, please fill out and return this form.

Name: _____

Date: _____

Location

Place-name / nearest population centre: _____

Post code: _____

Coordinates if available: _____

Circle coordinate system:

Finnish KKJ Zone 1 2 3 4 Long. and lat.

Can you see other oaks when you stand at the tree? _____

Approximately how many? 1-5 6-10 more than 10

Circle the tree's habitat

Forest Open ground Forest edge Other: _____

Tree

Circle estimated height

Under 2 m 2-5 m 5-10 m Over 10 m

Circle estimated trunk circumference at chest height

Thinner than your wrist (Under 16 cm) Between wrist and thigh (16-55 cm) Thicker than your thigh (Over 55 cm)

Answer in the autumn: how much of the foliage is yellow?

Less than a fifth Between a fifth and half More than half

Age of tree if known: _____

Origin of tree if known (planted or wild):_____

Please write your comments, observations etc. overleaf !