

Community composition and species richness of parasitoids infesting *Yponomeuta* species in the Netherlands

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Abstract

Parasitoid assemblages infesting *Yponomeuta* species in the Netherlands were investigated. Parasitoid species richness and community composition were related to host species, habitat, temporal and spatial variation. Both community structure and species richness did not differ among habitats. There was no significant difference in species richness between years (1994 and 1995) but there was a significant difference in community composition. Community composition and species richness both differed among host species, although this latter result was solely due to the host species *Y. evonymellus*. There was no significant relationship between community similarity and distance. These results indicate that the parasitoids of the moth genus *Yponomeuta* in the Netherlands appear to form a spatially stable, but temporally variable community. Most of the variation in community structure was, however, related to the host species. The marked difference in parasitoid species richness and community composition of *Y. evonymellus* when compared to the other species warrants further study.

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Introduction

Both deterministic and stochastic processes are believed to be important in structuring patterns of community similarity in natural environments (Robinson et al. 2000). Recently, however, there has been considerable debate on the relative importance of these processes in explaining patterns of beta diversity (Bell, 2001; Condit et al., 2002; Duivenvoorden, 2002; Whitfield, 2002; Wright, 2002). In a study of small mammals, for example, in Australia, Williams et al. (2002) found that community composition was strongly related to vegetation structure. Likewise, urban bird species richness was found to be independent of the surrounding periurban landscape and city size in North America and Europe, and to primarily depend on local habitat structure (Clergeau et al., 2001). Distance played an important role in predicting patterns of plant community similarity in Central and South American lowland rainforests (Condit et al., 2002). On the other hand in a study of freshwater invertebrates in Israel neither distance nor environmental variables explained a significant amount of variation in levels of community similarity (Spencer et al. 2002).

The present study concerns the parasitoid community of the moth genus *Yponomeuta* in the Netherlands. Parasitoids are significant components of many communities. Assemblages of parasitoids, for example, can have important regulatory effects on their host species and have been shown to be able to control the population dynamics of their hosts

by stabilizing otherwise chaotic growth and decline cycles (Driessen and Hemerik, 1991; but see Begon et al., 1995).

Parasitoid species, furthermore, appear to recognise their resources as a single niche axis. Each parasitoid species entering a community involves sequential divisions of resources. There appears to be a stepwise random division of resources at each addition of a species so that these communities are minimally structured, which implies that biotic processes such as competition and predation play a small role in the development of parasitoid assemblages. The most important ecological factor for parasitoids is probably the stage of the host utilised so that by partitioning even a single host a potentially rich parasitoid community can develop (Naeem and Hawkins, 1994).

The focal parasitoid community used in this study is the guild of parasitoids infesting the moth genus *Yponomeuta*. The importance of distance, habitat, and host species in structuring patterns of diversity in the parasitoids that feed on *Yponomeuta* moth species in the Netherlands is assessed. The relationship between distance and community similarity is assumed to be a predictor of community-wide dispersal rates (Spencer et al. 2002). All *Yponomeuta* hosts are univoltine and feed on various shrub and tree species, often becoming a pest when ornamental or crop species (e.g., apple or plum) are consumed. The *Yponomeuta* host species and their parasitoids are generally very common, conspicuous (they often spin large webs around shrubs or trees), easy to sample, and identify (Martouret et al., 1966).

The questions addressed with this study are: \

1. Is the community similarity of the parasitoids infesting *Yponomeuta* moths related to temporal variation (between years), habitat, and/or host species?
2. Is there a relationship between community similarity and distance?
3. Is the species richness of the parasitoids infesting *Yponomeuta* moths related to temporal variation (between years), habitat, and/or host species?

Material and method

Sampling and localities

Sampling took place in the Netherlands in a wide variety of habitats ranging from urban parks to forests (Table 1). The *Yponomeuta* host species were often sympatric, and the webs left by feeding caterpillars were easily observed and sampled.

In order to estimate community similarity and species richness of parasitoid assemblages infesting *Yponomeuta* spp. populations of four host species, *Y. cagnagellus*, *Y. evonymellus*, *Y. padellus* and *Y. rorellus* were sampled in the Netherlands during 1994 and 1995. The sampling localities and geographic position in the Netherlands are listed in Table 1. All host-populations with less than ten parasitoid individuals and 100 host individuals were excluded from the analyses. Various sites and host-populations were sampled in each locality. During the collection, the habitat (dune scrub, rural hedgerow, forest and urban park) and plant species on which the host was found were noted. Each site was checked for all potential *Yponomeuta* hosts. In the analysis, each host species per site is considered a single sample. *Yponomeuta* larvae from each host population were raised indoors at the Institute for Biodiversity and Ecosystem Dynamics (Amsterdam). The larvae were bred in enclosed cages on the same food plant species upon which they were found. Caterpillars or pupae with parasitoids (these were easily distinguished from healthy caterpillars or pupae) were selected and placed in large tubes so that the emerging parasitoids could be collected.

The following parasitoid species were collected from *Yponomeuta* host populations: *Ageniaspis fuscicollis* (gregarious primary parasitoid of eggs), *Diadegma armillata* (solitary polyphagous primary parasitoid from third instar on), *Herpestomes brunnicornis* (solitary parasitoid from fifth instar on), *Agria mamillata* (polyphagous predator consuming fifth instar larvae and pupae), *Mesochorus vittator* (solitary secondary parasitoid of *Diadegma armillata*), *Tetrastichus evonymellae* (gregarious primary and secondary parasitoid from third instar on), *Agrypon anxium* (solitary polyphagous primary parasitoid from third instar on), and *Pimpla turio-*

Table 1. Host populations (Pop.), Sites, localities (within sites), year of sampling, host, and host plant (plant) of local parasitoid communities collected in the Netherlands. Hab: habitat type, Total: number of caterpillars collected from a population, %par: percentage of caterpillars infected by a parasitoid, Rich: rarefied species richness ($n = 10$), Yp: number of host species present in a locality.

Pop.	Site	Locality	Year	Host	Plant	Hab	Total	%Par	Rich	Yp
C94.1	Awd duinen	Zuid	1994	<i>Y. cag</i>	<i>E. europeaus</i>	Dune	1371	2.4	1.0	2
C94.100	Meijendel	Bierlap behind Uitkijk	1994	<i>Y. cag</i>	<i>E. europeaus</i>	Dune	280	15.7	2.5	3
C94.17	Bergschenhoek	Lage Bergse Bos	1994	<i>Y. cag</i>	<i>E. europeaus</i>	Rural	395	9.4	1.0	4
C94.3	Awd duinen	Midden	1994	<i>Y. cag</i>	<i>E. europeaus</i>	Dune	1710	2.8	1.0	2
C94.32	Malden	Heemtuin; rand achteraan	1994	<i>Y. cag</i>	<i>E. europeaus</i>	Forest	262	18.3	1.6	4
C94.41	Wageningen	Bornse steeg; beh. stud. Flat	1994	<i>Y. cag</i>	<i>E. europeaus</i>	Rural	104	28.9	1.3	3
C94.5	Awd duinen	Noord	1994	<i>Y. cag</i>	<i>E. europeaus</i>	Dune	410	3.7	1.0	2
C94.84	Nieuwekerk	Parallelweg zuid	1994	<i>Y. cag</i>	<i>E. europeaus</i>	Rural	317	13.6	1.0	2
C95.27	Almelo	Schapendijk	1995	<i>Y. cag</i>	<i>E. europeaus</i>	Rural	2099	21.0	1.0	2
C95.32	Maashees	Camping	1995	<i>Y. cag</i>	<i>E. europeaus</i>	Rural	1215	10.1	1.1	2
C95.41	Wageningen	Blauwe Bergen	1995	<i>Y. cag</i>	<i>E. europeaus</i>	Park	402	17.4	1.4	3
C95.49	Bergschenhoek	Lage Bergse Bos	1995	<i>Y. cag</i>	<i>E. europeaus</i>	Rural	1580	12.7	1.0	4
C95.53	Meijendel	Bierlap (behind) and Uitkijk	1995	<i>Y. cag</i>	<i>E. europeaus</i>	Dune	516	6.6	1.3	3
C95.80	Amsterdam	Rembrandtpark	1995	<i>Y. cag</i>	<i>E. europeaus</i>	Rural	387	13.7	1.0	4
E94.107	Amsterdam	Louwesweg	1994	<i>Y. evo</i>	<i>P. padus</i>	Rural	1512	2.2	3.1	2
E94.34	Malden	Heemtuin; vennetje	1994	<i>Y. evo</i>	<i>P. padus</i>	Forest	279	11.2	3.6	4
E94.47	Wageningen	Bornse Steeg; road	1994	<i>Y. evo</i>	<i>P. padus</i>	Rural	658	5.1	3.2	4
E94.49	Oosthuizen	Oude sportveld	1994	<i>Y. evo</i>	<i>P. padus</i>	Rural	234	7.3	2.0	3
E94.77	Amsterdam	Rembrandtpark	1994	<i>Y. evo</i>	<i>P. padus</i>	Dune	662	2.7	4.0	4
E94.79	Rijnsaterwoude	Geluidswal N 207	1994	<i>Y. evo</i>	<i>P. padus</i>	Rural	397	6.9	3.5	2
E94.85	s Gravendeel	Sportpark	1994	<i>Y. evo</i>	<i>P. padus</i>	Park	155	20.6	1.0	1
E94.96	Amsterdam	Anna's Hoeve	1994	<i>Y. evo</i>	<i>P. padus</i>	Rural	2173	7.0	2.5	4
E94.98	Meijendel	Uitkijk	1994	<i>Y. evo</i>	<i>P. padus</i>	Dune	1817	1.0	4.5	3
E95.23	Almelo	Wateregge	1995	<i>Y. evo</i>	<i>P. padus</i>	Rural	305	6.2	1.0	1
E95.24	Nieuwe ter Aa	Bosdijk	1995	<i>Y. evo</i>	<i>P. padus</i>	Rural	1873	6.4	1.0	2
E95.38	Malden	Heemtuin; vennetje	1995	<i>Y. evo</i>	<i>P. padus</i>	Forest	511	2.0	3.0	4
E95.45	Almelo	Bosrand	1995	<i>Y. evo</i>	<i>P. padus</i>	Forest	7526	4.6	2.5	1
E95.47	Bergschenhoek	Lage Bergse Bos	1995	<i>Y. evo</i>	<i>P. padus</i>	Rural	3216	0.9	1.9	4
E95.51	Meijendel	Uitkijk	1995	<i>Y. evo</i>	<i>P. padus</i>	Dune	4002	0.7	1.0	3
E95.60	Amsterdam	Rembrandtpark	1995	<i>Y. evo</i>	<i>P. padus</i>	Park	2723	1.7	1.0	4
E95.74	Hoge Veluwe	Kemperberg; in de bocht	1995	<i>Y. evo</i>	<i>P. padus</i>	Forest	286	14.6	4.1	2
PA94.64	Hoge Veluwe	Heidebloem; 7+8 'eetplaats'	1994	<i>Y. pad</i>	<i>A. lamarckii</i>	Forest	124	28.2	1.0	2
PA95.67	Hoge Veluwe	Heidebloem '6', Zandweg	1995	<i>Y. pad</i>	<i>A. lamarckii</i>	Forest	109	19.2	2.5	2
PB95.84	Malden	Zeevliegveld B	1995	<i>Y. pad</i>	<i>S. aucuparia</i>	Forest	129	10.9	1.0	4
PC94.103	Rottebandreef	Rottebaandreef, Molenlaan	1994	<i>Y. pad</i>	<i>C. mongyna</i>	Rural	193	10.9	1.0	3
PC94.4	Awd duinen	Midden	1994	<i>Y. pad</i>	<i>C. mongyna</i>	Dune	144	13.9	1.0	2
PC94.67	Hoge Veluwe	Kemperberg '10'	1994	<i>Y. pad</i>	<i>C. mongyna</i>	Forest	100	15.0	1.0	2
PC94.80	Rijnsaterwoude	Geluidswal N 207	1994	<i>Y. pad</i>	<i>C. mongyna</i>	Rural	176	10.2	1.9	2
PC95.28	Almelo	Schapendijk	1995	<i>Y. pad</i>	<i>C. mongyna</i>	Rural	557	24.8	1.1	2
PC95.36	Malden	Heemtuin; rand vooraan	1995	<i>Y. pad</i>	<i>C. mongyna</i>	Forest	311	26.7	1.0	4
PC95.48	Bergschenhoek	Lage Bergse Bos	1995	<i>Y. pad</i>	<i>C. mongyna</i>	Rural	818	21.8	1.0	4
PC95.52	Meijendel	Bierlap (behind, Uitkijk	1995	<i>Y. pad</i>	<i>C. mongyna</i>	Dune	840	3.6	1.0	3
PC95.75	Amsterdam	Rembrandtpark	1995	<i>Y. pad</i>	<i>C. mongyna</i>	Park	766	4.3	1.0	4
PS94.83	Nieuwekerk	Parallelweg zuid	1994	<i>Y. pad</i>	<i>P. spinosa</i>	Rural	408	32.5	1.2	2
PS95.33	Maashees	camping	1995	<i>Y. pad</i>	<i>P. spinosa</i>	Rural	147	21.1	1.0	2
PS95.37	Malden	Heemtuin; rand vooraan	1995	<i>Y. pad</i>	<i>P. spinosa</i>	Forest	174	8.6	1.0	4
R94.18	Bergschenhoek	Lage Bergse Bos	1994	<i>Y. ror</i>	<i>Salix sp.</i>	Rural	115	30.4	1.0	4
R94.76	Amsterdam	Rembrandtpark	1994	<i>Y. ror</i>	<i>Salix sp.</i>	Park	381	6.8	2.0	4
R95.50	Bergschenhoek	Lage Bergse Bos	1995	<i>Y. ror</i>	<i>Salix sp.</i>	Rural	208	35.1	1.0	4
R95.50	Bergschenhoek	Lage Bergse Bos	1995	<i>Y. ror</i>	<i>Salix sp.</i>	Rural	117	13.5	1.2	4
R95.83	Amsterdam	Rembrandtpark	1995	<i>Y. ror</i>	<i>Salix sp.</i>	Park	1611	6.7	1.0	4

nellae (solitary primary parasitoid of pupae). More detailed descriptions of the parasitoid species can be found in Dijkerman et al. (1986).

Analyses

Community composition

Variation in the overall community composition among habitats (dune scrub, rural hedgerow, forest and urban park), among host species, and between years (1994 and 1995) was tested for significance using ANOSIM (non parametric analysis of similarities) with the package PRIMER (Clarke and Gorley 2001). ANOSIM is roughly analogous to standard univariate ANOVAs, and tests the variance within and between a priori defined groups in ordinate space. A Bray-Curtis similarity matrix was used for across-site comparisons. The ANOSIM R statistic values are an absolute measure of how separated the groups are. A zero (0) indicates that there is no difference among groups, while a one (1) indicates that all samples within groups are more similar to one another than any samples from different groups (Clarke and Gorley, 2001). The results of the ANOSIM are presented in addition to a multidimensional scaling ordination based on the same similarity matrix. Three one-way ANOSIMs were used where I tested for significant differences among habitat type, host type, and between years (for details and description of ANOSIM see Clarke and Gorley, 2001). The relationship between community similarity and distance was tested with the RELATE option of PRIMER, which tested for a significant relationship between two matrices of which one was a matrix of community similarity based on the Bray-Curtis similarity matrix and the other was a matrix of distances between pairs of host-populations. The distances were based on Universal Transverse Mercator (UTM) coordinates from each site.

Species richness

Rarefaction analysis was conducted, due to differing sampling sizes per locality, with the DIVERSE

option of the PRIMER program (Clarke and Gorley, 2001). The sample size used for rarefaction of parasitoids per host population was 10 individuals. Species richness among habitat types, hosts, and years was tested with a Kruskal Wallis test using Statistica for Windows (Statistica for Windows, 1996)

Results

Community composition

There was no significant difference in community composition among local parasitoid communities from different habitats ($R_{\text{ANOSIM}} = -0.038$, $P = 0.282$), but there was a significant difference between years ($R_{\text{ANOSIM}} = 0.07$, $P = 0.012$) and among local parasitoid communities from different host species ($R_{\text{ANOSIM}} = 0.126$, $P = 0.002$). Pairwise comparisons showed that there was no significant difference among local parasitoid communities of *Y. cagnagellus*, *Y. padellus*, and *Y. rorellus*, (cag-pad: $R_{\text{ANOSIM}} = 0.003$, $p = 0.370$; cag-ror: $R_{\text{ANOSIM}} = -0.092$, $p = 0.692$; pad-ror: $R_{\text{ANOSIM}} = -0.095$, $p = 0.647$) but local communities of *Y. evonymellus* differed significantly from the three other hosts (Figure 1; evo-cag: $R_{\text{ANOSIM}} = 0.331$, $p < 0.001$; evo-pad: $R_{\text{ANOSIM}} = 0.274$, $p < 0.001$; evo-ror: $R_{\text{ANOSIM}} = 0.164$, $p = 0.062$). There was no significant relationship between community similarity and distance

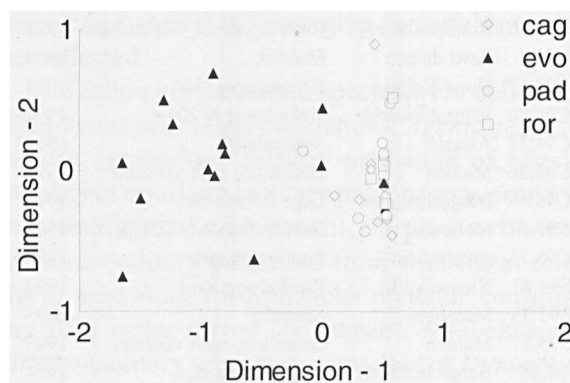


Fig. 1. Multidimensional scaling ordination based on the parasitoids of the *Yponomeuta* species complex in the Netherlands. cag: *Y. cagnagellus*, evo: *Y. evonymellus*, pad: *Y. padellus*, ror: *Y. rorellus*. The first two dimensions of the analysis are shown.

Table 2. Summary of statistics of species richness grouped by host species, year, and habitat.

Factor	Variable	Median	Minimum	Maximum	Lower quartile	Upper quartile	Quartile range
Host species	<i>Y. cagnagellus</i>	1.00	1.00	2.54	1.00	1.33	0.33
	<i>Y. evonymellus</i>	2.49	1.00	4.46	1.00	3.53	2.53
	<i>Y. padellus</i>	1.00	1.00	2.48	1.00	1.07	0.07
	<i>Y. rorellus</i>	1.00	1.00	1.98	1.00	1.24	0.24
Year	1994	1.33	1.00	4.46	1.00	2.54	1.54
	1995	1.00	1.00	4.06	1.00	1.29	0.29
Habitat	Dune	1.00	1.00	4.46	1.00	2.54	1.54
	Rural	1.04	1.00	3.53	1.00	1.93	0.93
	Forest	1.62	1.00	4.06	1.00	3.00	2.00
	Park	1.00	1.00	1.98	1.00	1.38	0.38

($Rho = 0.007$, $p = 0.394$). The parasitoid species and populations sampled during this study and their abundance in each site is presented in Appendix I.

Species richness

There was no significant difference in species richness of local parasitoid communities among habitat types (Kruskal Wallis Test: $H = 1.584$, $p = 0.663$) or between years (Kruskal Wallis Test: $H = 3.155$, $p = 0.076$), but there was a significant difference among hosts (Table 2; Kruskal Wallis Test: $H = 13.236$, $p = 0.005$). The parasite guild infesting *Y. evonymellus* was significantly richer than the guilds infesting the other host species.

Discussion

The community composition of the parasitoids infesting *Yponomeuta* spp. did not differ significantly between very different habitats (e.g. city parks versus dune scrub) and there was no significant relationship between community structure and distance. Community composition did, however, differ marginally between years, but the main difference in community composition was between host species. Importantly, in both community composition and species richness there were no significant differences among populations from the host species *Y. cagnagellus*, *Y. padellus*, and *Y. rorellus*, but popu-

lations from *Y. evonymellus* deviated significantly from all of the other host species.

Taking only the three host species *Y. cagnagellus*, *Y. padellus*, and *Y. rorellus* into account this indicates that the parasitoid assemblages of these species are locally impoverished (generally only a single parasitoid species present) and spatially homogenous indicating that there is no dispersal limitation of these parasitoids in the Netherlands. Despite the fact that the *Yponomeuta* species here share no food plants they may (because of the overlap in eclosion; Martouret et al., 1966) engage in apparent competition (Holt and Lawton, 1993; Thomas et al., 1997) through their shared parasitoids.

The difference in community composition and species richness between *Y. evonymellus* and the other species may be related to the ability of this species to suppress levels of infestation by the specialist parasitoid *Ageniaspis fuscicollis*. Dijkerman (1987) showed that the level of infestation of *A. fuscicollis* was much lower in *Y. evonymellus* than in the other *Yponomeuta* host species. The exact mechanism of this suppression is unknown but may involve some sort of encapsulation of the eggs of *A. fuscicollis*. Apparently the ability of *Y. evonymellus* to reduce levels of parasitization by *A. fuscicollis* has created opportunities for the other generalist parasitoids to thrive and locally coexist in this host species.

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Appendix I. Number of parasitoids, grouped by species, collected per host population. Populations (Pop.) are same as in Table 1.

Pop.	<i>Ageniaspis fuscicollis</i>	<i>Diadegma armillata</i>	<i>Herpestomes brunnicornis</i>	<i>Agria mamillata</i>	<i>Mesochorus vittator</i>	<i>Tetrastichus evonymellae</i>	<i>Agrypon anxium</i>	<i>Pimpla turionellae</i>
C94.1	33	0	0	0	0	0	0	0
C94.100	16	0	3	25	0	0	0	0
C94.17	37	0	0	0	0	0	0	0
C94.3	48	0	0	0	0	0	0	0
C94.32	44	0	0	4	0	0	0	0
C94.41	29	0	0	1	0	0	0	0
C94.5	15	0	0	0	0	0	0	0
C94.84	43	0	0	0	0	0	0	0
C95.27	441	0	0	0	0	0	0	0
C95.32	122	0	0	0	0	0	1	0
C95.41	67	3	0	0	0	0	0	0
C95.49	200	0	0	0	0	0	0	0
C95.53	33	0	0	1	0	0	0	0
C95.80	53	0	0	0	0	0	0	0
E94.107	7	21	0	0	2	3	0	0
E94.34	6	18	0	1	4	2	0	0
E94.47	9	19	0	0	3	0	2	0
E94.49	0	13	0	0	4	0	0	0
E94.77	6	7	0	0	2	1	1	0
E94.79	3	11	0	0	10	0	3	0
E94.85	0	32	0	0	0	0	0	0
E94.96	8	106	2	0	35	0	0	0
E94.98	1	9	0	4	1	2	0	1
E95.23	19	0	0	0	0	0	0	0
E95.24	120	0	0	0	0	0	0	0
E95.38	8	1	0	1	0	0	0	0
E95.45	234	90	0	0	1	21	0	0
E95.47	26	2	0	0	1	0	0	0
E95.51	28	0	0	0	0	0	0	0
E95.60	46	0	0	0	0	0	0	0
E95.74	3	6	0	0	4	15	14	0
PA94.64	35	0	0	0	0	0	0	0
PA95.67	17	2	0	0	2	0	0	0
PB95.84	0	0	0	0	0	0	0	14
PC94.103	21	0	0	0	0	0	0	0
PC94.4	20	0	0	0	0	0	0	0
PC94.67	15	0	0	0	0	0	0	0
PC94.80	15	0	3	0	0	0	0	0
PC95.28	137	1	0	0	0	0	0	0
PC95.36	83	0	0	0	0	0	0	0
PC95.48	178	0	0	0	0	0	0	0
PC95.52	30	0	0	0	0	0	0	0
PC95.75	33	0	0	0	0	0	0	0
PS94.83	131	0	0	1	0	1	0	0
PS95.33	31	0	0	0	0	0	0	0
PS95.37	15	0	0	0	0	0	0	0
R94.18	35	0	0	0	0	0	0	0
R94.76	19	0	7	0	0	0	0	0
R95.50a	28	0	0	0	0	0	0	0
R95.50b	40	0	0	1	0	0	0	0
R95.83	108	0	0	0	0	0	0	0