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Community assemblage of the Carabidae fauna in newly created habitats

René Verhagen, Rudy van Diggelen, Rikjan Vermeulen

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Removal of topsoil on former agricultural fields resulted in a rapid reduction in soil fertility. Insight into the general principles determining invertebrate faunal community assemblage after removal of topsoil was studied by correlating assemblage of the carabid community ten years after topsoil removal, to traits related to abiotic preferences, dispersal ability and the relative abundance of species. Special emphasis is put on the animal species characteristic of low production communities (target species). Results showed that newly exposed sites were rapidly colonized by Carabidae. Both abiotic preference and dispersal ability to some extent influenced community assemblage. Over time the importance of abiotic conditions on community assemblage increased, whilst dispersal restrictions seemed to decrease. During the first ten years chance factors appeared to be of major importance on community assemblage.

Isolated restoration sites were almost exclusively colonised by flying species. Restoration of the characteristic invertebrate carabid fauna of low production communities thus requires the presence of source populations in the immediate surroundings. It is concluded that restoration of low production communities on former agricultural land is an effective conservation method for carabid beetles, particularly for endangered, non-flying, large species.

Key words: Assembly rules; Dispersal ability; Isolation; Low productivity community; Restoration; Species conservation; Topsoil removal.

René Verhagen. Stichting Willem Beijerinck Biologisch Station, Kanaaldijk 36, 9409 TV Loon, The Netherlands; Community and Conservation Ecology Group, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

Rudy van Diggelen. Community and Conservation Ecology Group, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

**Rikjan Vermeulen. Stichting Willem Beijerinck Biologisch Station, Kanaaldijk 36, 9409 TV Loon, The Netherlands.*

**: Corresponding author*
email: rikjan@biological-station.com

INTRODUCTION

Ecological restoration is a relative new, proactive way to counteract community and species decline. The aim of restoration is to improve conditions for specific plant and animal communities, and often involves manipulation of the physical and chemical environment. The ecological basis of this approach is the assumption that environmental factors and the composition or functioning of communities are closely related (Anderson, 1995; Hobbs & Norton, 1996). However, individual attempts to restore a specific target community do not always result in the desired outcome. To improve predictability of species composition after a restoration event, insight is required into the general principles of species assembly during the formation of communities (Belyea & Lancaster, 1999). The application of the concept of *assembly rules* may enhance the prediction of community species composition.

Assembly rules consist of a set of rules that relate to "species pools" (Pärtel *et al*., 1996; Zobel *et al*., 1998) and environmental constraints. The objective is to predict which subset of the regional species pool is likely to co-occur in a specified habitat (Keddy, 1992; Weiher & Keddy, 1999). Abiotic constraints and biotic interactions operate as filters on specific traits, eliminating those sets of traits that are not adapted to a specified habitat (Keddy, 1992). It has been suggested that by comparing the traits of species present with those of species absent from a particular habitat, it might be possible to reveal which traits are selected against, or are favoured. During the 1990's, removal of topsoil from agricultural fields has been undertaken in an attempt to restore the low production communities that previously occurred in the north of the Netherlands. Although it is possible to rapidly create appropriate physical and chemical conditions, this is not followed by complete development of the target plant communities (Verhagen et al., 2001). Colonisation appeared to be a slow process; in which particular rare species were significantly less successful at establishing permanent populations than common species (Verhagen, 2007). A consistent correlation was not found between any specific species trait and the population density of colonizing species, suggesting that stochastic processes are of major importance in determining species dynamics. Insight into the factors affecting faunal species assemblage after removal of topsoil is lacking thus far. Increased knowledge about this will enable the development of more accurate restoration strategies for fauna in the future (Luken, 1990; Marrs & Bradshaw, 1993). In order to obtain further insight, we studied the assemblage of the Carabid fauna after removal of topsoil. The taxonomic group "carabid beetles" (Carabidae, Coleoptera) encompasses a large, well-studied group of species (Dessender & Turin, 1989). Carabid beetles have been shown to respond rapidly to changes in abiotic conditions in just three to five years (Perner & Malt, 2003). Their presence is related to vegetation structure, but, in contrast to many other insect groups, is not dependent on specific plant species (Gardner, 1991). This means that the slow establishment of the target plant species is not limiting colonisation by carabid beetles. Within the group of carabid beetles large differences in dispersal ability can be found, but unlike the situation in many other terrestrial animals, these differences can be quantified with precision (Den Boer, 1977, 1990a).

To test whether colonisation by carabid beetles on newly created habitats is mainly constrained by abiotic filters, dispersal ability or is dependent on chance processes, we sampled eight sites where topsoil was removed. Some of the restoration sites were situated adjacent to a nature reserve which contained low-productivity plant communities. Other sites were in isolated locations within an agricultural landscape. We started the analysis with a search for specific traits which were favoured during the first ten years following topsoil removal. Then, we compared species traits between restored sites and adjacent nature reserves. Next, we analysed whether differences in species composition between isolated and non-isolated sites could be related to specific traits. Finally, we distinguished between good and poor coloniser species and analysed whether this could be related to differences in species traits. Because the goal of topsoil removal was to restore low-productivity plant communities, we carried out analyses using two different subsets of species. These were either, including all species or only using characteristic species of low production communities. This latter group is often referred to as the 'target species'.

MATERIAL AND METHODS

Study sites

The study was carried out at eight former agriculturally exploited sites on sandy soils in the northern part of the Netherlands (Fig. 1). Data on historical land use, isolation of the site in relation to existing heathland and existing vegetation are presented in table 1. Topsoil was removed between 1989 and 1995 with depth of removal varying from very superficial to over 50 cm. Consequently, soil fertility varied considerably between and within sites (Verhagen 2007), but in all sites soil fertility was comparable with that of low-productivity communities. Management after topsoil removal consisted of grazing by livestock. In addition, some of the sites were mown once a year.

Half of the restoration sites were located adjacent to existing nature reserves harbouring low production plant communities. The other half were isolated, surrounded by an agricultural landscape. Characteristic target beetle species have a discontinuous distribution through the landscape, but many other species can be found in a wide variety of habitats. The term 'isolation' therefore is used in this paper with respect to these target species only.

Sampling method

The Carabid community at the Hullenzand site was sampled regularly during the first ten years after topsoil removal. In addition, seven other sites where topsoil was removed, ranging from ten to fourteen years old, were sampled over a

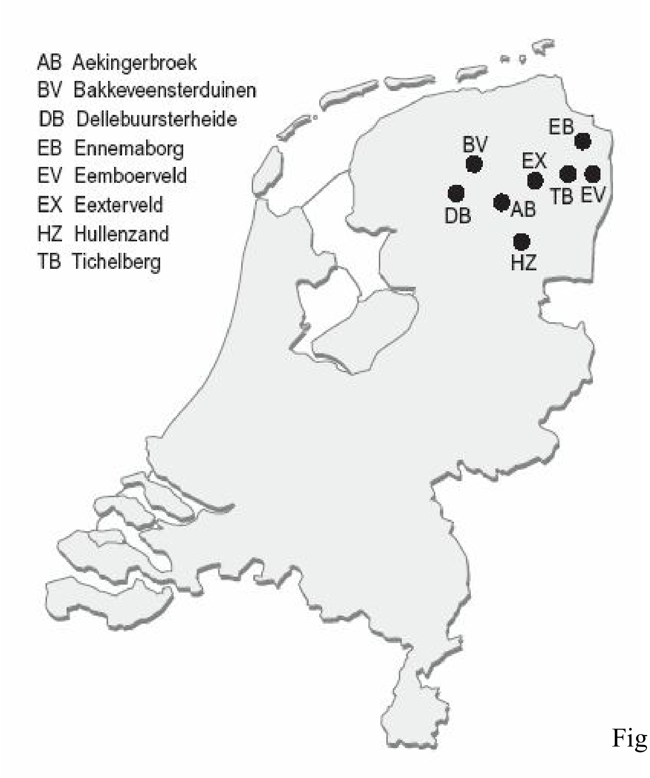

Fig. 1. Location of the study sites

Table 1. Characteristics of eight experimental sites. Vegetation characteristics are given for the location of the pitfall traps at each site.

Site	Coordinates	Size (ha)	Year of reclamation	Former agricultural exploitation	Year of top soil removal	Isolated from target communities	Characteristics of the existing vegetation
Aekingerbroek	52°55'N 6°18'E	20	Before 1920	Pasture	1992	No	Open, low grasses.
Bakkeveensterduinen	53°04'N 6°16'E	3	± 1930	Pasture	1989	No	Dense, low heather
Dellebuursterheide	52°57'N 6°08'E	25	± 1930	Arable and pasture	1993	No	Dense, tall grasses
Eemboerveld	53°02'N 7°01'E	10	1910 - 1930	Arable field	1991	Yes	Open, low herbs
Eexterveld	53°00'N 6°42'E	2	1940 –1955	Pasture	1994	Yes	Open, low grasses
Ennemaborg	53°11'N 7°01'E	7.5	Before 1900	Arable field	1992	Yes	Open, low grasses
Hullenzand	52°46'N 6°34'E	1.5	1940 –1955	Arable field	1993 - 1994	No	Open, low herbs
Tichelberg	53°01'N 7°00'E	2	Before 1900	Pasture	1992	Yes	Open, low herbs

period of one year. At the Hullenzand site two adjacent fields, where topsoil had been removed in 1992 and 1993 respectively, were sampled from March 1996 until March 1998 and again from March 2002 until March 2004. The other topsoil removal sites with nearby low production plant communities were sampled over a period of one year. The sites located at Delleburen, Ennemaborg, Eemboerveld and Eexterveld were sampled from March 2002 until March 2003. The remaining sites (Aekingerbrock, Bakkeveensterduinen, and Tichelberg) were sampled from March 2002 until March 2004.

Sampling was undertaken throughout the year using standard sets of five pitfall traps per site (Den Boer, 1977). Using this method about 95 % of the species, active within a radius of 50 m around the traps, are thought to be caught (Baars & Van Dijk, 1984). A pitfall trap consists of a plastic cup (diameter 10,5 cm, depth 15 cm), inserted in the soil with the upper rim at surface level. A ring mounted near the rim of the pitfall trap prevents beetles, which have been caught, from escaping again. Each pitfall trap contained a few ml of 4 % formalin, to rapidly kill the beetles and thus prevent large individuals from eating smaller ones. The cups were covered with a plastic roof at about 5 cm above the surface level. Pitfall traps were placed along a straight line, with a 5 m. interval between them. The traps were emptied every two weeks.

At the Hullenzand site, one restoration field and the nearby reference sites were sampled by a set of two square iron cans (30 x 20 cm, depth 30 cm) and a square funnel (same size) attached to a small container filled with 4 % formalin (Den Boer, 1977). In the square cans individuals were trapped alive. To keep out predators, the cans were provided with a wire net at 5 cm below the upper rim, and covered with a metal roof. The traps were placed at intervals of 10 m. along a straight line with the funnel in the middle. These traps were emptied every week. Carabid species were identified according to Boeken *et al.* (2002).

Species traits

We utilized species traits related to habitat preference, dispersal capacity and occurrence in the surroundings of the restoration sites, as described by Boeken *et al.* (2002).

It was not possible to derive *frequency* of regional occurrence from published data. However, the range of distribution of carabid beetles in the Netherlands and their local abundance are intimately linked (Kotze *et al.*, 2003). Widespread species are also locally abundant, whilst narrowly distributed species also tend to be rare locally. This implies that the number of grid cells (10 km x 10 km) occupied by a species in the Netherlands (Turin, 2000) gives an approximate indication of local frequency.

Habitat preference of a species is expressed as the *ecological characterisation* of species and their *ecological amplitude* (Turin *et al.*, 1991). Ecological characterisation indicates the type of habitat preferred by a species. We refer to species that were identified by Turin *et al.* (1991) as being restricted to the habitats raised bogs, heathlands, drifting sand areas and/or nutrient-poor grasslands as ‘target species’. The ecological amplitude gives an indication of the number of habitat types in which a species regularly occurs. This amplitude is expressed as a score between 1 and 10, whereby 1 indicates that the species is highly restricted to a certain habitat. Such specialised species are referred to as ‘stenotopic’. Species with a score of 10 are found in all kinds of habitats. Such species, which do not have a clear preference for a particular habitat, are known as ‘eurytopic’.

Carabid beetles disperse by flying or by walking. Species capable of flying can disperse over large distances, but only a restricted number of species has the *ability to fly.* Only those that have fully developed wings and flight muscles will be capable of doing so. In the case of some species, although they possess both fully developed wings and flight muscles, flight has never been observed. These species may not fly at all, or it may be a very rare phenomenon. In our analysis we only scored species as capable of flying, when it was indicated in Boeken *et al.*, (2002) that flight has been observed. Species without the ability to fly have to disperse by walking. Carabid beetles easily move out of their preferred habitat. After prolonged periods in unfavourable habitats, their behaviour changes into an extreme kind of obsessive walking in an arbitrary direction (Baars, 1979). The distance that species can traverse by walking is highly correlated with their *size.* Small species are limited in their walking distances to a few tens of metres whilst large species sometimes walk distances of up to one kilometre (Den Boer, 1977). Therefore size forms a good indication of the active-radius of non-flying species.

Data analysis

Data providing evidence about the occurrence of species were grouped per pitfall set. Analyses were carried out on qualitative data only, meaning that differences in the number of individuals between species were not taken into account.

For the Hullenzand site we analysed whether specific species traits had been favoured, or selected against, over time. Then we calculated yearly averages per trait and carried out trend analyses on these averages (curve fitting).

Species composition between reference sites and restoration sites were compared using DCA analysis (Canoco 4.5). Subsequent analysis

Table 2. Directional changes in traits during the first ten years after top soil removal in restoration site Hullenzand.

Trait	All species	Species of nutrient-poor conditions
Frequency	$y = -2.38x + 233.8$ ($R^2 = 0.54$; p ? 0.05)	n.s.
Ecological amplitude	n.s.	$y = -0.06x + 6.41$ ($R^2 = 0.59$; p ? 0.05)
# of flying species	n.s.	n.s.
# of non-flying species	$y = 0.57x + 6.0$ ($R^2 = 0.66$; p ? 0.01)	$y=0.27x + 1.14$ ($R^2 = 0.51$; p ? 0.05)
Size of non-flying species	$y = – 0.32x + 15.21$ ($R^2 = 0.57$: p ? 0.05)	n.s.

employed a Mann Whitney U test with exact probability to determine whether the number of species per ecological group and species traits, differed between the reference sites and restoration sites. We also analysed for differences between isolated and non-isolated sites using a Mann Whitney U test.

Species were classified as *good* or *poor colonisers*, by comparing catches over a period of one year on each restoration site with catches in the nearby reference nature reserve. This analysis was carried out only for the non-isolated sites. Good colonisers are characteristic species that were present in the restoration site with a population size at least 10 % of the population present in the nearby reference site. Poor colonisers were either completely absent in the restoration site or were present with less than 10 % of the population recorded in the nearby reference site. We analysed (for individual sites and pooling all sites together) whether traits of good and poor colonisers were evenly distributed over the classes of the trait (Mann Whitney U test with exact probability). This analysis was carried out including all species. It was not possible to separately analyse the group of target species because the number of species was too small to produce meaningful results.

All statistical calculations were performed using SPSS-PC.

RESULTS

Community assemblage over time

Almost 40 different carabid species were caught on the fields with removed topsoil within three years after its removal (Figure 2). The total number of species gradually increased over time up to ten years. About half of the species belonged to the group of eurytopic species. Over time, the number of eurytopic species was constant, whilst the number of target species increased from three to nine species. Species from other ecological groups occurred very rarely in the study sites, and therefore are not mentioned separately.

Changes in the community assemblage over time showed that the number of species not capable of flying increased, whilst the number of species

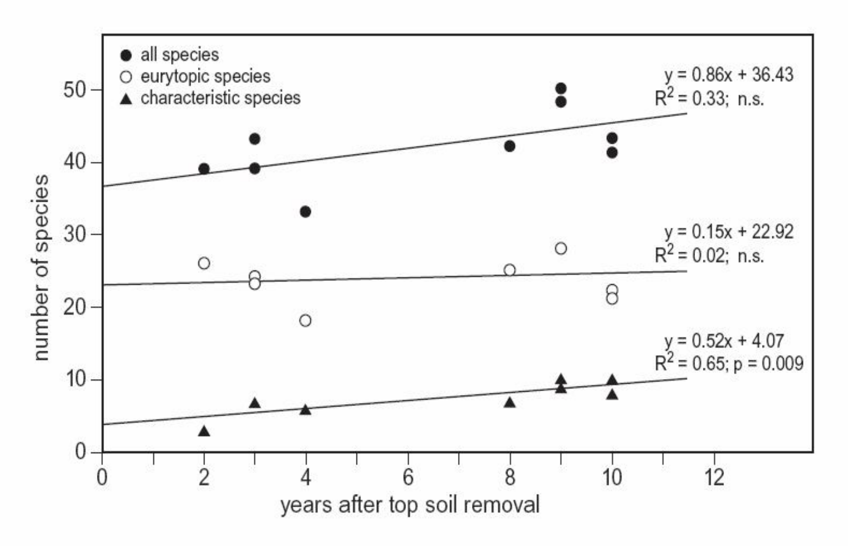

Fig. 2. The number of species trapped in the restoration site Hullenzand during the first ten years after top soil removal. Species are grouped according to their habitat preference (after Turin et al., 1991).

capable of flying remained constant (Table 2). This was true for all species but also for the target species alone. Including all species, the average frequency and body size of the non-flying species showed a decreasing trend. This indicates that less common and smaller species tended to colonise the restoration fields over time. Analysis of target species traits revealed a negative trend for ecological amplitude, so that in later years more stenotopic species were found in the restoration fields.

Comparing restoration and reference sites

Ten to fourteen years after restoration measures were applied, species composition in the restoration sites remained different from the adjacent target plant communities (Figure 3). The first axis, which explains almost 19 % of the variation, is related to the moisture status of the fields during summer. The wettest sites are plotted on the left and the drier ones on the right. The second axis, which explains 7 % of the variation, distinguishes between reference and restoration sites.

Comparison of the restoration sites with nearby reference sites revealed significantly less target species in the restoration sites (Table 3). The frequency of occurrence of the target species in the Netherlands was less in the restoration sites than in the adjacent reference sites, but species with large body size were more common. This indicates that in particular the relatively common, small species are under-represented in fields with removed topsoil. No statistically significant differences were found for the other traits.

Isolation effects

Comparison of the isolated restoration sites with the non-isolated sites revealed that the number of eurytopic species was the same in both (Table 4). However, isolated sites contained significantly less species typical of nutrient-poor conditions than the non-isolated sites., Almost all species characteristic of low production communities which were captured in isolated sites had the ability to fly and their number was similar to the non-isolated sites. Only two species could not fly.

Relating colonizing ability and species traits

Species which are good colonisers had a higher frequency than poor colonisers at three individual sites and for all sites combined (Table 5). At two sites the group of good colonizers contained significantly more species with the ability to fly than the group of poor colonizers. At the Hullenzand site and when all sites were combined together, body size of the good colonisers was significantly larger than for poor colonisers. Good and poor colonisers did not differ in ecological

Table 3. Differences between the total number of species, for two ecological groups and species traits between restoration sites and reference sites. Isolated restoration sites are not included in the analysis. Mean rank scores, Mann-Whitney U score and exact probability (n=20, except for the parameter size of non-flying species, where n=16).

				Species of nutrient poor conditions				
	# of species of nutrient poor conditions	# of eurytopic species	Total # of species	Frequency	Ecological amplitude	# of flying species	# of non-flying species	Size of non-flying species
Restoration sites	6.83	9.05	9.86	7.91	11.05	9.00	8.23	11.50
Reference sites	12.17	12.28	11.28	13.67	9.83	12.33	13.28	5.50
M-W U.	16.50	33.50	42.50	21.00	43.50	33.00	24.50	8.00
p-value (2-tailed)	0.032	0.234	0.617	0.031	0.670	0.202	0.057	0.009

Table 4. Differences in total number of species, for two ecological groups and species traits between isolated and non-isolated sites sampled in 2002 and 2003. Mean rank scores, Mann-Whitney U score and exact probability (n=16, except for parameter size of non-flying species where n=12).

				Species of nutrient poor conditions				
	# of species of nutrient poor conditions	# of eurytopic species	Total # of species.	Frequency	Ecological amplitude	# of flying species	# of non-flying species	Size of non-flying species
Non-isolated	9.28	9.11	9.06	8.33	8.22	7.39	9.61	5.50
Isolated	4.30	4.60	4.70	6.00	6.20	7.70	3.70	1.00
M-W U.	6.50	8.00	8.50	15.00	16.00	21.50	3.50	0.000
p-value (2-tailed)	0.032	n.s.	n.s.	n.s.	n.s.	n.s.	0.009	n.s

Table 5. P-values (2-tailed) for differences in species traits between the good and poor colonisers for the four non-isolated sites and all four sites together. In brackets, the number of good and poor colonisers.

Site	Frequency	Ecological characterization	Ecological amplitude	Ability to fly	Size of non-flying species
Aekingerbroek (57 / 16)	0.004	0.030	n.s.	0.027	n.s.
Bakkeveensterduinen (35 / 18)	0.013	n.s.	n.s.	0.013	n.s.
Dellebuursterheide (35 / 7)	0.031	n.s.	n.s.	n.s.	n.s.
Hullenzand (65 / 29)	n.s.	n.s.	n.s.	n.s.	0.005
All sites together (99/26)	<0.0001	n.s.	n.s.	n.s.	0.044

preferences, except at the Aekingerbroek site. At this site the group of good colonising species encompassed significantly more target species than the poor colonisers.

DISCUSSION

Community assembly

Removal of topsoil includes the removal of the entire top layer, containing all adults, larvae and eggs of the carabid fauna. Despite this, we caught a large number of carabid species on the restoration sites within two years. Kaufman (2001), Wagner & Fischer (2003) and Glück & Fischer (2003) found a similarly rapid colonisation of new sites by several different invertebrate taxa. This indicates that newly created habitats are rapidly colonised by the ground-dwelling fauna. The assemblage of the Carabid beetle community over time showed a gradual shift towards species adapted to nutrient-poor soil conditions. This accounted for both the number of characteristic species, as well as the individual population size of these species. In particular the characteristic species, *Poecilus lepidus*, *Agonum sexpunctatum* and *Amara equestris* increased in number over the period of monitoring. Over the same time period, the number of individuals of eurytopic species decreased, suggesting that abiotic conditions are important in structuring community assembly.

However this idea is not supported by comparison of good and poor colonising species. The latter analysis suggests that differences in dispersal ability seem to be more important in determining community assemblage. Species with the ability to fly colonised the restoration sites quickly, whilst colonisation by non-flying species was delayed. Sampling newly embanked polders revealed that species capable of flying were much more likely to colonise these sites than species lacking this ability (Den Boer, 1970, Meijer, 1974). Flying individuals might even cross distances of over 25 km (Den Boer, 1970). Because colonisation of isolated sites characterised by low-productivity communities was almost entirely restricted to flying species only, this result emphasises the importance of nearby source populations for those species lacking the ability to fly (De Vries *et al.*, 1996). A distance of over 500 m between heathlands is sufficient to ensure that Carabid species communities are isolated from each other (De Vries *et al.*, 1996).

Even when source populations are present nearby, colonising ability is influenced by dispersal ability. Non-flying, but large (30 mm) species can cross a distance of over one kilometre during their active season, whilst small (3 mm) species can disperse over several tens of metres at a maximum (Den Boer, 1977; 1990a). Thus small, non-flying species in particular are poor colonisers. In contradiction to this conclusion, five years after the restoration of wildflower meadows, Blake *et al.* (1996) found that mean body size. of carabid beetles in restored wild flower meadows was smaller than in reference sites. In our study, an increasing number of average species were found on the restoration sites over time.

Heijerman & Turin (1989) found that the assembly of carabid beetles in different types of forest showed greater similarity with the carabid beetle community that occurred nearby rather than the type of forest. This suggests that dispersal limitation is a major constraint for the assembly of carabid communities, at least in the beginning. We conclude that rare species will require, in general, more time for colonisation than common species, because the number of dispersing individuals is smaller (Den Boer, 1970). This conclusion is in agreement with the evidence about colonisation of newly embanked polders, where, although dispersal ability and habitat preference were important factors for

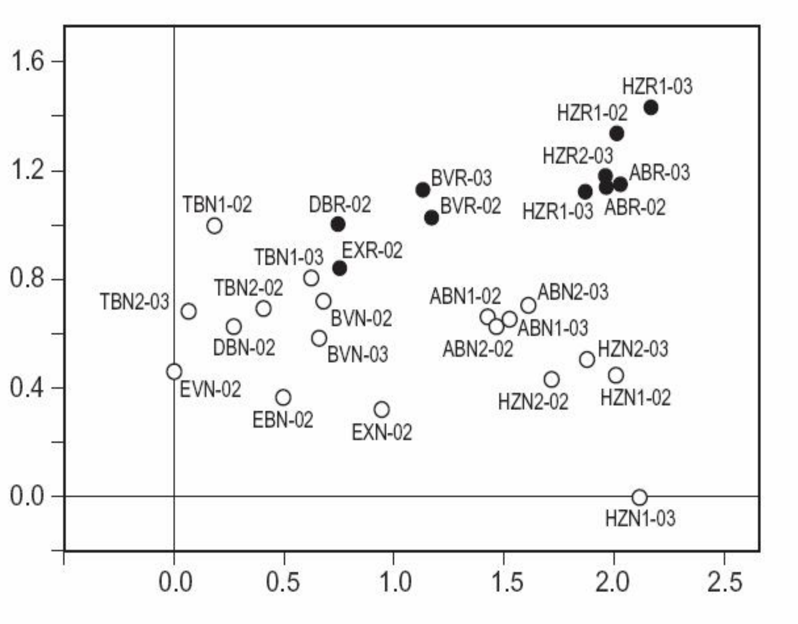

Figure 3: DCA analysis of the restoration areas in comparison with the reference sites including all species (species are log transformed).
The first two positions of the sample codes stand for sampling site (cf. Figure 1), the next whether the sample is from a reference site ('R') or a restoration site ('N') and the last two for the year of sampling.

colonisation, common species clearly prevailed (Haeck *et al.*, 1980).

Restoration of nutrient-poor communities

Removal of the topsoil resulted in a rapid establishment of target carabid species. Also several characteristic plant species established quickly (Verhagen *et al.*, 2001), in contrast to the slow reduction of soil fertility by annual haymaking on former agricultural fields. The latter management leads to a very low establishment rate of characteristic carabid beetles (Van Dijk, 1986) and plant species (Bakker & Elzinga, 2002). This shows that removal of topsoil is a fast and efficient way to speed up the restoration of nutrient-poor communities on former agricultural soils.

Compared to the vegetation, a higher proportion of the local species pool of target carabid species (on average, 70 %) established in the first decade than for the plant species (on average, 30 % (Verhagen *et al.*, 2001). We therefore conclude in agreement with Perner & Malt (2003), that invertebrates can be better indicators of short term change due to habitat restoration than plant communities. This is mainly due to differences in dispersal characteristics between carabid and plant species. Dispersal by many plant species is usually restricted to distances of a few metres from the parent plant, and long-distance dispersal is a rather rare phenomenon (Bullock & Clarke, 2000; Jongejans & Telenius, 2001). Thus only small numbers of propagules reached the topsoil removed sites (Verhagen *et al.*, 2003), and limited seed dispersal is considered to be a major constraint for natural vegetation restoration (Bakker & Berendse, 1999). Each year dispersal by walking or flight is a recurrent phenomenon in all carabid species (Den Boer, 1979). Several species characteristic of nutrient-poor conditions therefore can colonise the restoration sites without difficulty. Compared with vegetation, restoration of the characteristic carabid heathland community and probably the arthropod fauna in general (Den Boer, 1990a), will be much less restricted by dispersal limitations and therefore proceed more quickly.

Despite this, the number of characteristic carabid species is significantly smaller in the restoration sites than the adjacent reference heathlands ten years after restoration measures. The absence of target species after restoration measures have been applied is often related to the absence of source populations in the surroundings (Vermeulen et al., 1997; Van Duinen *et al*, 2003), but our results show that even in the presence of local source populations species might be lacking for more than a decade.

Implications for species conservation

Populations do not survive for eternity. Den Boer (1990b) estimated that the survival time of single interaction groups for most carabid species ranged from 9 to 40 years. Spreading the risk of extinction over several interconnected and differentially fluctuating groups, in contrast, results in almost unrestricted survival as unoccupied patches can be easily recolonised (Den Boer, 1990a; Den Boer & Reddingius, 1996). Recolonisation thus plays an essential role in the survival of a species. However, the number of suitable habitats that are occupied by carabid species with restricted dispersal, in the currently fragmented landscape of North West-Europe, is small compared to species with high dispersal capacity (Mabelis, 1986; Opdam *et al.*, 1993). The continued survival of many species with restricted dispersal is threatened. For the carabid fauna in particular, large, stenotopic non-flying species associated with open, nutrient-poor communities are decreasing (Desender & Turin, 1989; Kotze & O'Hara, 2003). Those species with intermediate dispersal ability are threatened not only because of loss of habitat, but also due to habitat fragmentation (Den Boer, 1985, Turin & Den Boer, 1988). A high proportion of individuals of these species will emigrate from suitable patches, but only a few will be able to reach new patches in the currently fragmented landscape. There is an interesting comparison with butterfly species. Those of intermediate mobility have declined more severely than species with high or low mobility (Thomas, 2000).

Our study suggests that carabid species of intermediate dispersal ability colonise restoration sites more easily than species with low dispersal ability. Restoration of low-productivity communities on former agricultural fields therefore seems to be a particularly effective method to increase the area occupied by these large, threatened species, and also to reconnected isolated populations.

Implications for spatial planning

An important prerequisite for restoration of the target carabid fauna is the presence of source populations in the immediate surroundings, but this does not guarantee a rapid recovery of the desired fauna. Only large reserves with good and stable environmental conditions are capable of maintaining viable populations of nearly all species. The most endangered species in particular are missing from smaller reserves (De Vries *et al*., 1996). The same situation was found for spiders (Hopkins & Webb, 1984).

Comparison of the species composition in the reference sites used in this study with two large heathlands areas in the North of the Netherlands revealed that several characteristic species characteristic of nutrient-poor conditions were even missing in these smaller reference sites. Because invertebrates fulfil a crucial part of the ecosystem in many food networks (Borro et al., 1989), this might also have important consequences for other species groups (Larochelle, 1980; Esselink et al., 1994; Pettersson et al., 1995; Kuper et al., 2000). Restoration efforts, therefore, should focus on connecting isolated nature reserves with the remaining large areas, but even then colonisation by species with low dispersal power will require several decades. In situations where nutrient-poor conditions can be created over large areas, but connections with existing large reserves cannot be established, active re-introduction of species with restricted dispersal powers should be considered.

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