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Distribution of carabid beetles in agroecosystems across spatial scales – A review

Konstantin B. Gongalsky, Francisco J. Cividanes

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The review focuses on the questions (1) how does the spatial heterogeneity of landscape influences carabid biodiversity, and (2) what are the main factors causing this biodiversity across nested spatial scales (study point – plant association – landscape level). The analysis of recent literature indicates that the spatial distribution of carabids differs at various spatial scales, and the factors responsible for the distribution are different. At the study point level most of the communities exhibit high variability of population density and diversity, which has no correlations with soil, and sometimes, vegetation, parameters. Most of the factors that contribute to formation of the communities are stochastic, simply because patches of a factor are much smaller than the size of a distinct carabid community. At the level of plant association, soil factors begin to play the role in driving the communities. At this level, litter depth, micro-climate and vegetation composition are the main factors. At the landscape level, geological factors, such as topography, landscape geochemistry, and history are playing important roles. As a conservation measure, spatial heterogeneity should be kept at all spatial scales at the same time to maintain carabid biodiversity in agricultural areas.

Key words: Carabidae, Spatial distribution, Habitat fragmentation, Species loss, Geostatistics, Biodiversity; Agroecosystems

Konstantin B. Gongalsky. A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Leninsky pr., 33, Moscow, 119071, Russian Federation. E-mail: kocio@mail.ru

Francisco J. Cividanes. Paulista State University, Dept. Fitossanidade, Via de Acesso Prof. Paulo Donato Castellane, 14.884-900, Jaboticabal, SP, Brazil

LAY-OUT

1. THE SPATIAL STRUCTURE OF AGRICULTURAL LANDSCAPE

1.1. The concept of nested spatial layers

The spatial heterogeneity of organisms is well known and is one of the main features of the reaction of aboveground biota to environmental factors. Spatial soil ecology (Ettema, Wardle, 2002) is a modern direction of soil animal studies involving all components of soil biota, including carabid beetles. The studies on spatial distribution are among the main aspects of agroecology, because the results obtained at relatively small areas are recommended for application at administrative provinces or even larger areas (Dalgaard et al, 2003). Another reason to study spatial variability of pedobionts is to maintain invasive species, many of which could be pests, that requires modern and adequate protection.

Scale is one of the basic concepts in geography, determining both the precision of estimates, and the methodological apparatus that enables to achieve such accuracy. At various spatial scales, the accuracy is achieved by means of different methods. One of the basic prerequisites in the studies of distribution of a resource (e.g. animals, plants, integral parameters of their communities) is the size of the area that has to be estimated. Depending on aims, a researcher deals with different scale layers that have distinct geographic interpretation, namely, the order of magnitude of an area. Hence, environment may be considered as a nested hierarchic structure. For example, Magurran (1988) proposed a concept of the layers of the spatial distribution of biodiversity. The minimal unit in consideration she proposed is **study point**, the level where a researcher works in the field. The layers of higher hierarchical status deal, in fact, with the data received at the study point level. A study point usually acquires less than 10 m^2. The latter may be sampled in multiple replications across a variety of locations, but still only these data are used in extrapolations. This is why the data sampled at this layer provide the baseline information on relations between the abiotic and biotic components of ecosystems, and allow extrapolating regularities discovered to higher spatial layers. Some factors may be more important at different layers.

The second layer that we consider is **the layer of plant association**. It has larger geometric size, from few to thousands m^2, depending on relief and other, mainly geographical, factors. At this layer there is no possibility to discover relations between factors at the study point level (not taking into account raw data), since cartographic generalization hides the local variability of data. The **layer of landscape** is a higher level of generalization that includes information on the total quantity of plant associations within a landscape. The size of landscape level varies from 10^7 to 10^9 m^2. Nested relation between the layers may be found in Ettema and Wardle (2002), where every upper layer carries information about the lower ones (Fig. 1).

Keeping this logic, **the regional level** emerges, that is, in fact, a field of study of biogeography. This is the level that operates different methodology and isn't really developed in entomology. Hence, we omit considering this level and higher, up to global, ones.

1.2. Ecological structure of agricultural landscape

An agroecosystem is a spatially heterogeneous or patchy landscape (Weibull et al., 2003; Gabriel et al., 2006). It is worth separating three different zones within an agricultural field: the central part of the field, the field edge, and the adjacent unploughed (border) zone. The complete assemblage of insects changes from the edge to the center, but usually the border differs from the edge even more. The reasons lay mostly in the microclimatic differences between these zones: the central part is the most dry zone and contrasting in the view of temperatures, while the border is the most balanced ecosystem in microclimatic conditions. In the temperate zone, the vegetation remaining for the winter period in the borders, serves as a refuge for insects living in the field, since they have no places to hide in the mown part. Insolation plays important role,

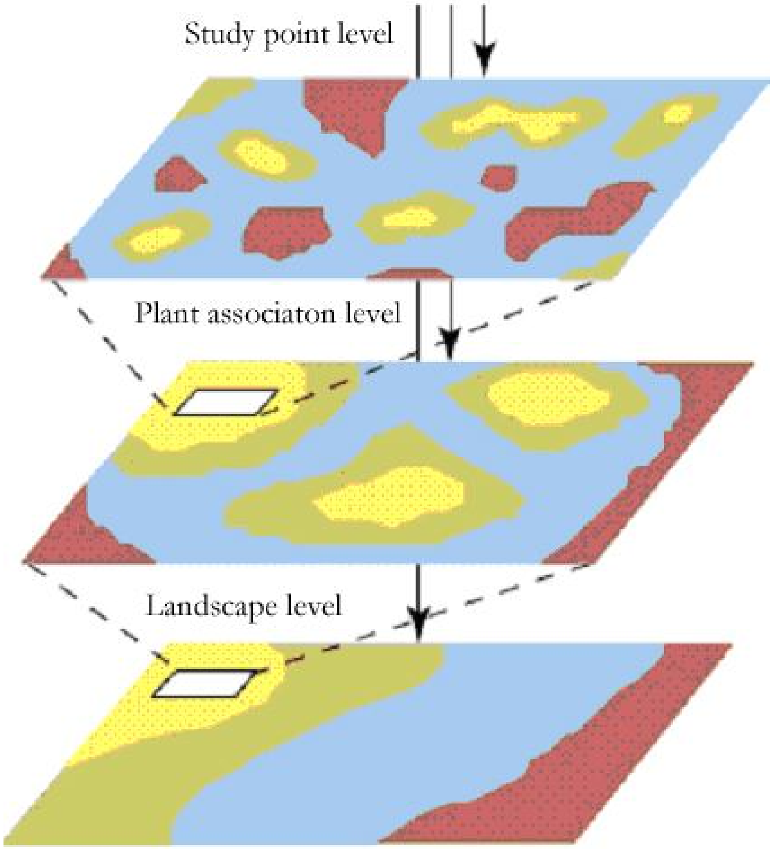

Fig. 1. Nested relations between the spatial levels (after Ettema, Wardle (2002), with changes).

especially in the beginning of season. In this case, the center of a field serves the most appropriate conditions for crops to grow (Tshernyshev, 2001; Olson, Wackers, 2007).

Insects inhabiting the field center come from different biotopes. Field borders are one of the most important sources for entomophagous insects suppressing pests. In general, the more biodiversity possesses an area the higher is the probability for predatory and parasitic insects to invade agricultural fields. Hence, landscape heterogeneity, supporting predators biodiversity in the fields, helps controlling pests (Thies, Tscharntke, 1999; Thomas et al., 2006).

Insect biodiversity is closely connected to that of vegetation (Kotze, O'Hara, 2003). The application of pesticides causes the growth of some perennial grasses that suppress other vegetation. Other way around, the elimination of root-gnawing insects increases the plantsÿ species number (Brown, Gange, 1992).

Biodiversity supports sustainability of natural ecosystems (Sankaran, McNaughton, 1999; Buchs, 2003), so it is supposed to do in ecologically managed agroecosystems. For this aim, baseline information for biodiversity assessment is needed. For example, in Canada, the basic biology and habitat requirements of almost all species occurring in agricultural habitats are known. Each species of beetle has special requirements based on soil type, moisture, pH, and light exposure. They are excellent indicators of habitat modification and of the quality of the environment. Because of their positive contribution to agricultural ecosystems, maintaining and developing their diversity by providing refuge habitats is recommended. Cropping sequence and type of crop influence ground beetle populations (Goulet, 2003). Numerous reviews on ecology of carabids in agroecosystems have been published in Europe and in Russia too (not referred here).

Understanding the spatial dynamics of insect distributions in farmland can provide insights into their ecological requirements and potential for management (Thomas et al., 2001). Identifying the scale, location and persistence of species' aggregations is an important step towards understanding the factors driving population distributions.

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2. CARABID BEETLES IN AGRICULTURAL FIELDS

Ground beetles, or carabids, occur in most of the agroecosystems of the world (Reichardt, 1977; Lövei, Sunderland, 1996; Davies, Margules, 1998; Morrone, 2006), and have been implicated as the predators of many pests, including aphids, lepidopterous larvae, and slugs. Most carabids are polyphagous, and some are primarily seed feeders (den Boer, 1977; Thiele, 1977; Lövei, Sunderland; 1996, Rainio, Niemelä, 2003; Honek at al., 2006). Species assemblage observed in a crop is determined by multiple factors, but usually comprises a limited number of abundantly active species, which may be common to many crop types. Crop type affects a carabid assemblage indirectly through cultivation practices and microclimatic changes. Soil cultivation affects carabid assemblage, but studies that compare ploughing with reduced tillage have shown varying results, according to local conditions. Pesticides, especially insecticides have localised and short-term effect, as many carabids rapidly re-invade sprayed crops. The long-term effect of pesticide usage at a landscape scale is, however, more difficult to predict, and many studies have documented decline in carabid diversity in wider countryside. Whilst fertiliser application is generally beneficial to carabids, comparisons of conventional and organic farming systems suggest that localised short-term variations in speciesÿ abundances are more important than the overall farming system used. Non-crop habitats are very important to Carabidae, as many use adjacent hedges and field margins for shelter, breeding or dispersal. But other features such as roads may act as barriers to dispersal (Holland, Luff, 2000).

There is a set of recent studies describing, in detail, the composition of carabid beetles communities during agricultural cycles in Europe (Petit, Burel, 1998; Molnar et al., 2000; Martin et al., 2001; de la Pena et al., 2003 etc). However, only a few of them took into account the spatial heterogeneity of landscape and aimed to consider beetlesÿ conservation under these conditions.

Recent agricultural practice in Europe includes organic and conventional farming, and ecologically-oriented agriculture. Broad interest arose, how these techniques influence carabids (Doring, Kromp, 2003; Doring et al., 2003; Melnychuk et al., 2003; Purtauf et al., 2005b). The majority of such studies are pilot observations, to what extent new farming practices influence carabids. We do not specially focus on this type of farming in this review, unless the results of the studies contribute to discovering the spatial structure of carabids in the fields.

The ground beetles have been often used as indicators of agricultural practices in ecological studies, but little is known about the spatial and temporal variation independent from the agricultural practices. In the studies of Irmler (Irmler, 2003; Irmler, Hoerens, 2003), five assemblages of ground beetles were differentiated, primarily by sand content of the soils and field size. Most species correlated positively with the sand content of the soils. Only two species, *Pterostichus* *melanarius* and *Loricera pilicornis*, showed a positive correlation with the field size. Higher species richness was observed on fields, which have practised for 30 years ecological farming. Comparing the two adjacent fields with ecological and conventional farming, no difference in species richness was detected. Four species showed higher abundance on the field with ecological farming. In this analysis of a long-term dataset of ground beetles did not respond to the cultivated plants, but only to the yearly climate conditions.

As compared with classic ecological observations, recently new methods were developed that allow unravelling connections between organisms and environment. Geostatistics, a methodology actively developing last decades in soil science (Webster, 1985; Jongman et al., 1995; Goovaerts, 1997; Ettema, Wardle, 2002) is now being applied to soil biology and entomology (Perry, 1995; Rossi et al., 1995; Rossi, 1996; Perry, Dixon, 2002). With the help of spatially arranged sampling design, many intriguing findings were observed (Franceschini et al., 1997; Holland et al., 1999, 2004; Kinnunen et al., 2001; Maudsley et al., 2002), that could not have appeared just few years before.

Thus, the spatial structure of agricultural landscape, and – at the local scale – of field, is one of the prevailing factors contributing the composition of carabid beetle communities of the field. The presence of remnants of forests, borders with large forested area and other sources of landscape heterogeneity are proven to be great impacting factors for the communities of beetles. The aim of this review is to analyse (1) does the spatial heterogeneity of landscape influences carabid biodiversity, and to what extend if it does; (2) what are the main factors of carabid biodiversity at various spatial scales.

3. DIVERSITY AND DISTRIBUTION OF CARABIDS AT THREE LANDSCAPE LEVELS

3.1. Study point level

There are numerous studies unravelling connection of carabids with environmental factors at the study point level, and within-population aggregations. The structure of the field is one of the main organizing factors of carabids in agricultural landscape. Thomas et al. (2001) found that each carabid taxon was aggregated most of the time, but different taxa aggregated in patches within the field and/or hedgerow to different and varying extents. The field boundaries were important for some species, either as the only habitat in which they occurred (*Amara spp.*), as the major focus of more widespread distribution (*Harpalus rufipes*), or as a seasonal refuge (*Nebria brevicollis*). Within the crop habitat, different species also occupied different areas, providing some evidence to suggest species packing in space. The spatial stability of patches suggests that future studies should focus on the detailed measurement of biotic and abiotic factors associated with patch location.

While studying fields in central Sweden, Wallin (1987) found that adult-overwinterers showed a seasonal migration between field edges or boundaries and the field, while some of the larval-overwinterers migrated to surrounding non-cultivated areas, such as woods and forests. Adult-overwinterers (*Bembidion lampros, Pterostichus cupreus,* and *Anchomenus dorsalis*) and the larval-overwintering *Harpalus rufipes* showed a preference for cereal fields, while the other tested larval-overwinterers (*Epaphius secalis* and *Pterostichus melanarius*), including the forest-species *Carabus nemoralis*, showed a preference for woods. *P. niger* was also tested, but exhibited no preference. The methodology of field tracing of individual animals in space was successfully applied in further studies (Walin, Ekbom, 1988; Charrier et al., 1997).

Volkmar et al. (2003) studied reduced soil tillage effects on arthropod assemblages (spiders, carabids and stapylinids). A field study was carried out 1998-2000 in Friemar (Thuringia, Germany). The carabids profited more than any other group of the predatory arthropods from reduced soil tillage. In 1998, the activity density of the Carabidae was more than 100% higher on the mulched plot in comparison to the ploughed plot. In conclusion, the findings suggest that reduced soil tillage does have a positive effect on predatory arthropods. Since many arthropods species feed on aphids and other insect pests, these results might also be interesting in terms of natural pest control.

The density of carabid population on an agricultural field depends upon the numbers of preys. This was demonstrated by the application of a newly invented geostatistical method, the SADIE-analysis: the patches of high carabid density collided with those of aphids (Winder et al., 2005). The same pattern was discovered by this group of investigators for carabid and plant viruses that they spread (Korie et al., 2000).
One of the influencing factors is the distribution of preys for carnivorous carabids. For example, ca. 11% of individuals of *Pterostichus melanarius* were slug-eaters (Bohan et al., 2000), but they strongly tended to associate with the patches of large slugs and their abundance fluctuations. Thus in a number of cases a direct analysis of pests in the field is required to decrease the amounts of pesticides applied (Archard et al., 2004).

A study on spatial distribution of the chrysomelid beetle, *Psylliodes chrysocephala*, carabids as its predators and collembolans as potential alternative prey revealed, that the chrysomelid beetle has only one potential consumer, *Trechus quadristriatus* (Warner et al., 2003). These two coincided in space that stimulated to increase abundance of predators in the fields. The same effects were observed when the spatial pattern of four carabids (*A. dorsalis*, *Amara similata*, *Nebria brevicollis,* and *Harpalus rufipes*) and their potential preys (larvae of *Dasineura brassicae*, that is a raps pest over Europe) was studied. Surprisingly, only *H. rufipes* aggregated with the pest larvae (Warner et al., 2000). Probably, misinterpretation was a result of spatial analysis since *H. rufipes* is a phytophagous species (Lindroth, 1992), which might gather on the crop.

As temperature, humidity, sunshine, rain, etc. have fundamental influences on the ecology of insects (Speight et al., 1999), microclimate is another possible cause of spatial variation in carabid population density within agricultural fields. The most important of these factors affecting carabids are temperature, humidity and light, which are affected by factors associated with soil and vegetation. It has to be emphasized that the microclimate of fields affects carabid prey numbers. Therefore, all these factors acting together and at the same time can create complex dynamics in the spatial distributions of carabids (Basedow, Kollat, 1997, Thomas et al., 2002).
The presence of weed cover and cover provided by the crop itself can affect the distribution of carabids, but findings from different studies are sometimes inconsistent (Thomas et al., 2002). Crist and Ahern (1999) suggested that the general distribution-abundance of *Harpalus pennsylvanicus* and *Calathus opaculus* can be explained by species response to the thermal environment as it varies among habitats and season. Temperature and precipitation appeared to be the major factors influencing carabid activity and species composition and abundance, which may change from year to year as influenced by weather conditions (Chen, Willson, 1996).

Within-population processes may influence spatial structure of a species distribution in space. For example, egg clutches cause aggregations of juvenile animals in the field in spring, which was shown by example of many groups (see: Hopkin, 1997, Pearce, Zalucki, 2006).

3.2. Plant assossiation level

At this level, habitat structure and mesoclimatic factors step on the scene. Fournier and Loreau

(2001) compared three kinds of habitats: small remnants of native forests, recent hedges and barley crops, in order to investigate their respective roles in the maintenance of carabid-beetle diversity in a 950-ha area of an intensive agricultural landscape. Carabid faunas in remnants differed weakly from these found in hedges and crops. In particular, small remnants had few typical forest carabid species and a large number of open-area or ubiquitous species. Different approaches in the measurement of alpha and beta-diversity (classical indices, and additive partitioning of Simpsonÿs index) showed similar results: hedges supported a high diversity but habitat types were quite similar overall, with weak differences between open and closed or disturbed and undisturbed habitats. A comparison of species dispersal powers in the various habitat types showed that species with a low dispersal power were rare in all habitats. However, wing development measured on two dimorphic species revealed, that brachypterous individuals were mainly present in hedges, which were expected a priori to be more disturbed, than remnants hence less suitable for the establishment of populations with a low dispersal power. These results suggest that small remnants do not behave as ‘climaxÿ habitats in this intensive agricultural landscape, probably because of their small size and strong isolation. The interest of new undisturbed habitats, such as recent hedges, for the maintenance of carabid diversity at both the local and landscape scale is important.

Three types of spatial distribution of insects in the agrosystems of Moscow region were distinguished: the preference of field (obligate agrobionts), the preference of field margins (some facultative agrobionts, which are able to colonize fields), and relatively even distribution within all zones of agrosystems (eurybionts). The habitat preference in many objects altered during a season and might depend on the kind of crops (for instance, winter or spring cultures). During a season, most of the insects migrated from field margins to field edges and then to the center. Some coincidence of allocation patterns in phytophagous and entomophagous insects were observed (Soboleva-Dokuchaeva et al., 2000; Afonina et al., 2004). The results of Boivin and Hance (2003) and Saska (2007) support the concept of permeability where species characteristic of a habitat are also captured albeit at a lower rate in adjacent habitats.

The number of species decreased significantly with distance from the centre of the newly arranged hedge (Fournier, Loreau, 1999). The various species had different spatial patterns of total capture and absolute density. Four groups of species can thus be distinguished: species restricted to the hedge, species preferring the hedge, species preferring the crop, and species unaffected by the hedge. The respective roles of small-scale abiotic changes in habitat structure and differences in prey availability are discussed (Fournier, Loreau, 1999). The colonisation of new hedges towards a typical hedge fauna progresses very slowly. Small, 9-year-old hedges do not function well as stepping stones for the dispersal of epigeic forest and forest-edge arthropods, and only a small corridor effect could be established for the linear plantation strip. Remarkable differences in colonisation trends between beetle and spider species were found by Gruttke and Kornacker (1995).

In a study of French and Elliott (1999), species composition was most strongly influenced by season, followed by year, and then habitat (wheat vs. grassland). Ground beetles that reproduce in spring were separated from those producing young in autumn along the first axis of a canonical correspondence analysis (CCA). With the effects of season and year removed, ground beetles were classified with respect to habitat preference along axes one and two of a partial CCA. Based on the ordination by partial CCA, ground beetles were classified either as habitat generalists, wheat specialists, grassland specialists, or boundary specialists. Landscape structure was an important component in determining the spatial distribution of ground beetles.

The beetle *Pterostichus melanarius* was unaffected by both fragmentation-scale and vegetation-composition manipulations. These findings highlight the challenge of developing a predictive theory of the effects of vegetation diversification on assemblages of predators in agroecosystems (Banks, 1999). The composition and spatial arrangement of perennial and annual crops in the agricultural landscape may be important to long-term population dynamics of carabids caused by their feeding requirements (Bommarco, 1999).

Significant differences in the overwintering densities of predatory carabid and staphylinid beetles and spiders occurred on an ‘islandÿ grassy bank habitat composed of blocks of grasses, within and between winters during a 7-year study in England (MacLeod et al., 2004). Over the period of study, the beetle bank maintained its role in providing overwintering habitat for polyphagous predators and carabid diversity has increased since the bank was first established. Beetle banks were therefore shown to contribute to conservation biodiversity in an agroecosystem.

Carabids of different trophic status react on landscape simplification by different ways. Purtauf et al. (2005a) studied the response of carabid species richness and density to landscape simplification (measured as percentage cover of non-crop habitat surrounding each study site) in 36 wheat fields using pitfall traps. The number of species from different trophic groups declined with increasing landscape simplification in the order: carnivores > phytophages > omnivores.

3.3. Landscape level

It was suggested by Noss (1983) that management of a landscape mosaic would provide a more efficient conservation strategy than the management of single sites. This suggestion is in accordance with the ‘habitat heterogeneity hypothesisÿ, which assumes that structurally complex habitats - comprising spatial scales from patch to landscape - may provide more niches and ways of resource exploitation and thus increase species diversity (MacArthur, Wilson, 1967; Tews et al., 2004). In this context, Dauber et al. (2005) conclude that agri-environment schemes for the conservation of biodiversity in cultivated landscapes have to secure management for both habitat quality and heterogeneous landscape mosaics.

Spatial distribution of carabids was connected to the field edges in a landscape with large fields more than that in a landscape with the small ones. Carabids differed in their distribution depending on their seasonal reproduction type and dispersal abilities. The beetles with the spring reproduction and those easily dispersing were more differently distributed across a variety of habitats (Bilde, Topping, 2004).

Judas et al. (2002) analysed the spatial distribution of 12 carabid species across a topographically variable area of ca. 4 km^2 within a landscape of continuous beech forests. All interpolations produced more or less patchy map patterns, while no pattern was exactly reproduced between years. Carabid species distribution at the landscape level was differentiated into four types: random, weak gradient, distinct gradient and restricted area. Maps for species with distinct gradients or restricted distributions were correlated between all years, while maps for species with random patterns were mostly uncorrelated. Distinct distribution gradients and restricted distribution areas could be attributed to a topoclimatic differentiation of the landscape. Thus, for some carabid species, microclimatic habitat associations scale up to distributions within a landscape. Eyre et al. (2004) have shown on the example of Great Britain that carabids, which typically occur on elevated areas, are better indicators of landscape characteristics. Species with coastal preferences were poorly modelled and predicted to occur throughout lowland Britain whilst a number of species occurring in southern Britain were predicted to occur in Scotland.

The regional diversity of temporary wetland carabid beetles was analyzed by Brose (2003) for six landscapes of 10 km^2 each. The relative importance of landscape features and cultivation intensity for the regional diversity was compared. Total species richness was correlated with the mean soil-indices that were used as indicators of cultivation intensity. These results do not corroborate concepts of using indices of landscape structure as biodiversity indicators, but the importance of cultivation intensity cannot be emphasized strongly enough.

Loreau et al. (2003) proposed that biodiversity provides spatial insurance for ecosystem functioning by virtue of spatial exchanges among local systems in heterogeneous landscapes. They explored this hypothesis by using a theoretical metacommunity (sensu: Hanski, 1998, 2005) model with explicit local consumer-resource dynamics and dispersal among systems. The model showed that variation in dispersal rate affected the temporal mean and variability of ecosystem productivity strongly and nonmonotonically through two mechanisms: spatial averaging by the intermediate-type species that tends to dominate the landscape at high dispersal rates, and functional compensations between species that are made possible by the maintenance of species diversity. The spatial insurance effects of species diversity are highest at the intermediate dispersal rates that maximize local diversity. Knowledge of spatial processes across ecosystems is critical to predict the effects of landscape changes on both biodiversity and ecosystem functioning and services.

Habitat fragmentation, one of the main factors causing species loss (Collinge, 2000; Kotze, O'Hara, 2003; Magagula, 2003), is now enhancing notwithstanding that the society have faced and realized the problem of biodiversity loss. Habitat fragmentation negatively affects carabid beetles in forested landscapes, too (Abildsnes, Tommerås, 2000).

In this context, lots of studies propose the establishment of artificial vegetation patches (Thomas, 1991, 1992; Duelli, Obrist, 2003; Ulrich et al., 2004) and field margins (Tschernyshev, 2001; Koivula et al., 2004; Woodcock et al., 2005) that could maintain biodiversity of carabids within a homogeneous agricultural landscape. However the efficiency of creating too small islands would be low: they will host not-mature communities (Zalewski, 2004) that are not enough effective in biological control of pests. It was shown (Ostman et al., 2001a,b) that landscape simplification directly decreases numbers of biological control agents, and the carabids among them.

The study of Purtauf et al. (2004) proves the need for sustaining arable farming in marginal landscapes to preserve the particularly species-rich carabid communities of arable land. Moreover, the rapid establishment of grassland communities indicates that 10–15-year cycles of low-intensive farming and grassland cultivation might be sufficient to maintain carabid communities of both arable land and grassland. Burel et al (2004) concluded that species survival in those fine grained agricultural landscapes depends on processes operating at the site scale and defining habitat quality, and processes operating at the landscape and/or metapopulation scale such as landscape modifications in connectivity and habitat availability.

4. CLOSING REMARKS

Spatial distribution of carabids differs at various spatial scales, and the factors responsible of the distribution are also different. At the study point level most of the communities exhibit high variability of population density and diversity, which has no correlations with soil, and sometimes, vegetation, parameters (Table 1). Most of the factors that contribute to formation of the communities are stochastic, simply because patches of a factor are much smaller that the size of distinct carabid community. When reaching the level of the plant association, soil factors begin to play the role in driving the communities. At this level, litter depth, stone/pebble content in the soil, and vegetation composition are the main factors. From the other hand, at the landscape level, geological factors, such as relief, landscape geochemistry, and history are playing important roles.

Table 1. Main factors influencing carabid communities in agricultural landscape on various scales.

Spatial layer	Dimension	Main factors
Study point	$< 10^1$	Stochastic
Plant assossiation	10^2-10^4	Soil parameters (litter depth, stone content), vegetation structure, microclimate
Landscape	10^7-10^9	Relief, landscape geochemistry, history of human activity

General conclusion is that commensurate factors act at each spatial level. In general, this can be distributed not only on spatial scale, but on temporal one too: the less resolution of spatial level the slower factors can be distinguished by its help. For example, effect of litter addition can be seen at a forest clearing, whilst an agricultural history of a region is detectable by only faunal changes of carabids. This allows applying chronosequences of communities instead of long-term studies (Pickett, 1989; Zaitsev et al, 2006).

As a conservation measure, spatial heterogeneity should be kept at all spatial scales at the same time to maintain carabid biodiversity (Niemela, 2001; Hunter, 2002; Chust et al., 2003; Wilson et al., 2004).

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