

Mobility of *Pterostichus melanarius* among different vegetation types

Thijs Strik (S4031571) & Oleta van Son (s4008286)

Supervisor: Raymond Klaassen

08/06/2022

Introduction

Over the past years, insect species have been declining massively. According to a study by Sánchez-Bayo & Wyckhuys (2019) more than 40% of the insects are threatened with extinction. The main driver of this event is thought to be the intensification of agriculture. This involves farming on expanded scales, an increase in monocultural production, the intensive application of fertilizers and pesticides and the destruction of wildlife habitats (Raven & Wagner, 2021). As insects are the functional and structural base of many ecosystems, the immense extinction rates could have cascading effects on all life forms on earth (Sánchez-Bayo & Wyckhuys, 2019). A study by Albrecht et al. (2007) found that a decrease in species richness at lower trophic levels leads to a reduction in species richness at higher trophic levels. Besides, reduction in species richness at the lower levels decreases interaction at the higher levels even stronger. This indicates that habitat destruction may be more detrimental to higher trophic levels than to lower trophic levels. Moreover, insects and other invertebrates play a key role in agricultural systems as they perform functions such as nutrient cycling, pollination, and biocontrol (Norris, 1994).

The European Union has set up certain measures through the Common Agricultural Policy (CAP) to preserve biodiversity and at the same time support farmers in their way of living (Pe'er et al. 2017). One important aspect of these programs is the introduction of set-aside field strips. Set-aside field strips are usually sown with grasses and herbs on areas of arable land and function as semi-natural habitats that are directed to biodiversity conservation. Besides enhancing biodiversity, the established field strips may also function as areas that favor predators that contribute to biological pest control (Haaland et al., 2011). A common species that thrives in set-aside field strips is the ground beetle. In general, these species are generalist predators that play an important role in reducing hemipterous pests, such as aphids, leafhoppers, and bugs (Symondson et al., 2002). A lot of research has been done on quantifying beetle diversity in relation to set-aside field strips. In many cases, beetle diversity in set-aside field strips is observed to be higher than in other field margin types or habitats (Pfiffner & Luka 2000; Kromp et al., 2004). However, whereas some studies found that the biodiversity of predatory arthropods in neighboring crop fields increases as an effect of the field strips (Hawthorne et al., 1998; McCabe et al., 2017), other studies found that an increase in biodiversity was limited to the field strips only (Smith et al., 2008). These contrasting results indicate that the exact role of set-aside field strips for ground beetles is still unknown.

Field strips may have different functions for ground beetles. It might function as a habitat where they reside throughout the year, or as a habitat from which they invade neighboring crop fields. Agricultural activities, such as plowing, can have detrimental effects on the survival of ground beetles. Therefore, when agricultural activity is high, ground beetles might disperse to neighboring field strips. How easily ground beetles switch from different habitats has not been quantified yet. Research by Woodcock et al. 2008 found that an important factor that influences beetle abundance is vegetation structure. Consequently, we could hypothesize that the edge to a crop field is more strongly perceived as a barrier if the structure of the crop differs more strongly from the structure of the vegetation in the set-aside field strip. These differences may ultimately explain the fluctuations in ground beetle abundance throughout the year in different crop fields. Windschut (2021) found that the most common species of *Carabidae* in Eastern Groningen, the location of our study, is *Pterostichus melanarius*. Moreover, *P. melanarius* functions well as a model species as it has an important function in natural pest control due to its unspecific predatory diet.

The following research question was investigated in this study: Are borders between set-aside field edges and crop fields stronger barriers for moving in *Pterostichus melanarius* if the crop vegetation differs more strongly from the set-aside habitat? To quantify this effect, dispersion between different habitats was monitored for *P. melanarius*. Two types of arable fields were used for this study: winter wheat fields and sugar beet fields. A study by Turin (2000) indicated that abundance of *P. melanarius* is low in poor, open habitats and high in biodiverse grasslands. As the vegetation structure of winter wheat fields is more comparable to field strips than that of sugar beet fields, we expect that the edge to wheat fields functions less as a barrier than the edge to beet fields. Moreover, as sugar beet fields are considered barren, open landscapes, we expect more movement from the crop field into the field strip.

Materials & Methods

Study framework

The study sites were established on the farm of P.H. Mulders between Zuidbroek and Muntendam in Eastern Groningen, the Netherlands. This farm is partially located on sandy and sandy-clay soil (Wageningen University, 2006). The majority of the farms in the area use forms of intense agriculture. P.H. Mulder performs a more sustainable way of farming as only one specific insecticide, which controls the Colorado potato beetle, is used. Moreover, the use of other pesticides has been reduced to the minimum and plowing has not been done for c.a. 15 years. Furthermore, at this farm, multiple field strips and other biodiverse areas have been established in the last decade.

The experiments in the winter wheat fields were executed on location A (figure 1) and is located on sandy-clay soil. The experiments in the sugar beet fields were executed on location B (figure 1) and is located on sandy soil. Beetle mobility was measured over a period of 2 weeks from 9/5/2022 until 20/5/2022. In this period there were small amounts of precipitation with zero rainfall on most of the dates and 10,1 mm and 17,9 mm of rainfall on 19/5/2022 and 20/5/2022, respectively. The daily average temperature fluctuated between 13.3 °C and 19.3°C over the whole period. This data was measured by nearby weather stations in Eelde and Nieuw Beerta (KNMI).

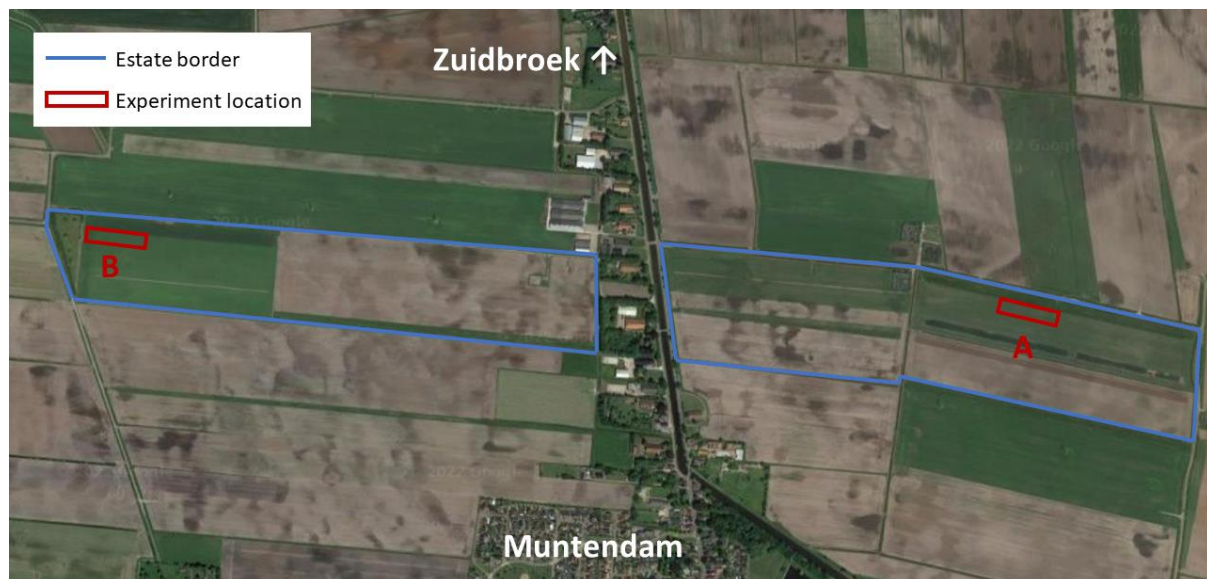


Figure 1: geographical location of experiments

Experiments

The experiments were performed in duplo in 2 different set-ups on 2 sites (A and B, figure 1). In set-up 1, dispersal was measured with a release point inside the arable field. In set-up 2, dispersal was measured with a release point inside the fieldstrip (figure 2). The set-up resembled a grid like structure to account for horizontal and perpendicular dispersal. Pitfall traps with a layer of vegetation were used to (re)capture the ground beetles. On the start of an experiment the pitfalls were emptied into a container, and 30 specimens were marked and released onto the designated release point. The experiments ran overnight since *P. melanarius* is a nocturnally active predator (Turin, H. 2000). The next day the pitfalls were emptied, and the recaptured specimens were counted. For each experiment 30 individuals of *P. melanarius* were captured, marked, and released. With an exception on 12/5/2022, on this day no sufficient beetles were captured, and the experiments were executed with 25 specimens. The experimental grids had a length of 3 m and a width of 2 m and contained evenly spaced-out pitfall traps (1 m between every trap). The experiments were not enclosed. However, every experiment was spaced out by at least 15 m, and the specimens were marked with distinct color patterns to be able to exclude between recaptures.

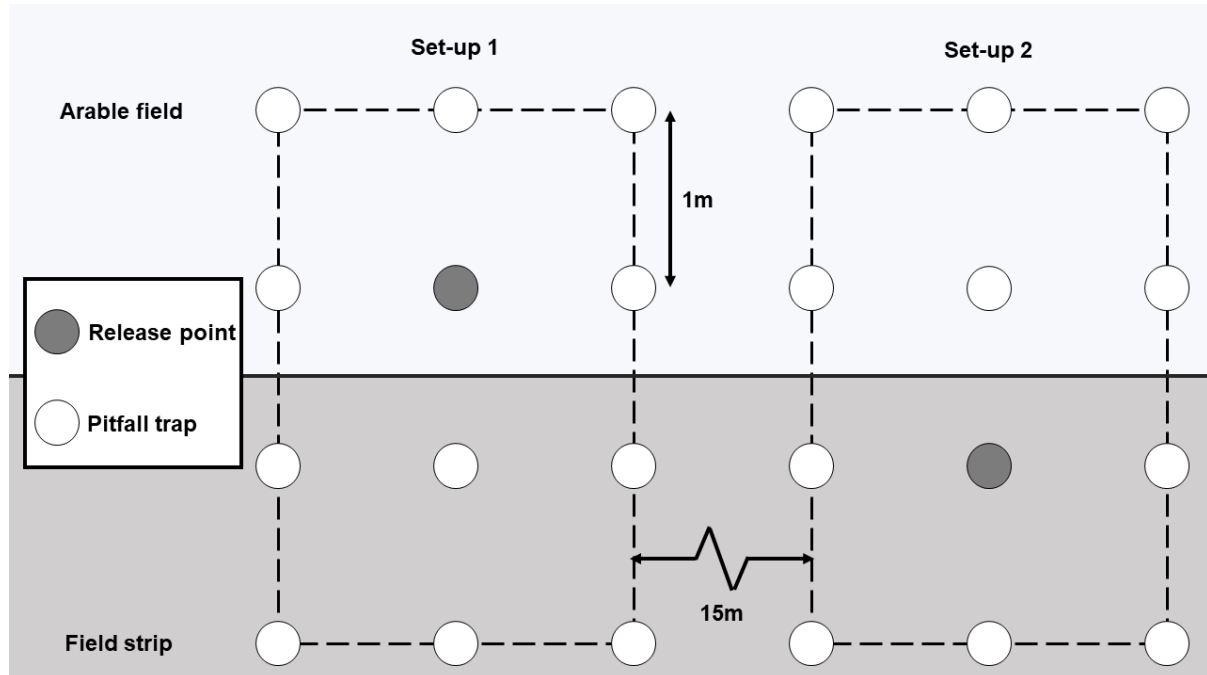


Figure 2: Set-ups of experiments

Marking techniques

A variety of different colors of nail polish was used to mark the specimens (HEMA, the Netherland). Nail polish tends to bind to keratin, a structural compound found in hair and nails among vertebrates (Fraser, 1972). Chitin, a structural compound found in exoskeletons of arthropods, is functionally comparable to keratin (Tang et al. 2015). Due to this structural similarity, nail polish is a fitting way to mark exoskeleton arthropods. *P. melanarius* features a sizable pronotum and elytra. These parts house surfaces well suited for nail polish marking by hand and offer the ability to mark the specimen with 3 different colors.



Image 1: Marking technique

Species studied

P. melanarius is the most abundant species of *Coleoptera* in the insect community in agriculture in eastern Groningen (Windschut, 2021). *P. melanarius* is characterized by its nocturnal activity and mostly hunts on bottom-dwelling arthropods such as ants, mites, larvae, and slugs. The development of the larvae occurs in autumn. In winter, when temperatures are just above freezing, *P. melanarius* has been found to be active at the surface in small numbers. However, higher abundance of *P. melanarius* are found when temperatures become higher. In June and July explosive growths are observed (Turin, H. 2000).



Image 2: *P. melanarius*

Data analysis

The data of the experiments over a period of 6 days were added up to establish sizable datasets. This results in 4 different experiments (n=1) with recaptures ranging between 11 and 35. The number of observed catches per pitfall was compared to the predicted number of catches by the theoretical null model (figure 3). To calculate whether the measured dispersal differs from the theoretical null model, chi-square tests and binomial distribution models were used. Moreover, to calculate the significance of the differences found in dispersal between the experiments, chi-square tests were executed. To account for multiple independent tests, the α -value needed to be adjusted. For this we used the Bonferroni correction. All the data was analyzed in Microsoft Excel.



Figure 3: The theoretical null model. The transparent circles indicate the pitfalls, and the colored circle indicates the release point. The numbers inside the pitfalls describe the chance that a recaptured beetle would fall in that certain trap, if mobility is random.

Results

Recaptures

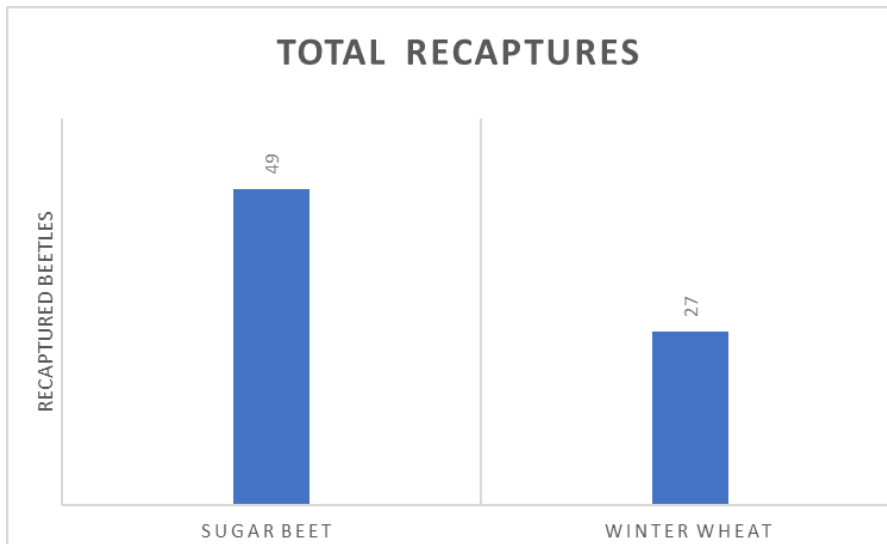


Figure 4: Total number of beetles recaptured per study site.

From the 1440 beetles that were released during the experiment, 49 (3.4 %) individuals were recaptured in the sugar beet study site, and 27 (1.2 %) were recaptured in the winter wheat study site (figure 4).

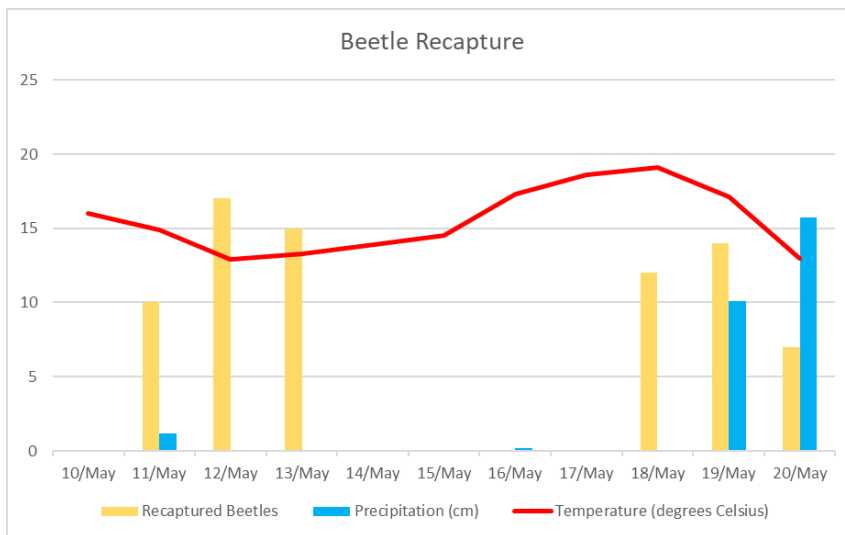


Figure 5: Beetle recaptures per day in relation to precipitation and temperature.

Beetle recapture measurements were only executed on May 11th, 12th, 13th, 18th, 19th and 20th. On the last day (20th of May) the number of recaptured beetles was notably low. During this day, and on the day before, precipitation was considerably higher than precipitation on the other measuring days (figure 5).

Dispersal: within the habitat or crossing the border

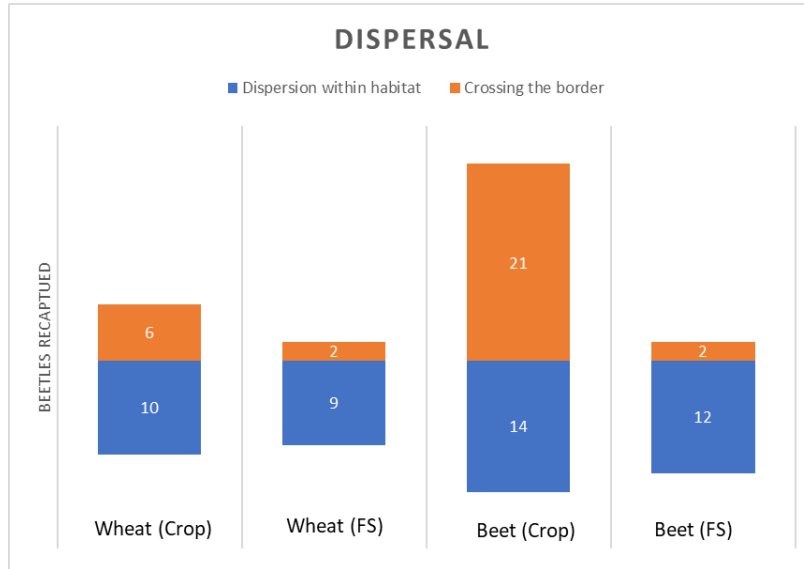


Figure 6: The number of beetles that dispersed within the habitat and the number of beetles that crossed the border at the four different experimental set-ups. The x-axis indicates the study site (Wheat or Beet) and the release point (Crop or Field Strip (FS)).

The number of individuals that crossed the border significantly differs between the four different experiments ($p= 6.4 \cdot 10^{-7}$). However, there was no significant difference found in dispersion within the habitat between the experiments ($p=0.7$) (figure 6).

Recaptures per pitfall: expected and observed

Table 1: The expected number of beetles recaptured per pitfall or grouped pitfalls if the beetles would disperse according to the null model. RP= Release Point.

Release point	Pitfall 1+3	Pitfall 2	Pitfall 4+6	Pitfall 5	Pitfall 7+9	Pitfall 8	Pitfall 10+12	Pitfall 11
Wheat, Crop	2,8	1,9	3,9	RP	2,8	1,9	1,7	1,0
Wheat, Field strip	1,2	0,7	1,9	1,3	2,7	RP	1,9	1,3
Beet, Crop	6,0	4,3	8,5	RP	6,0	4,3	3,8	2,1
Beet, Field strip	1,5	0,9	2,4	1,7	3,4	RP	2,4	1,7

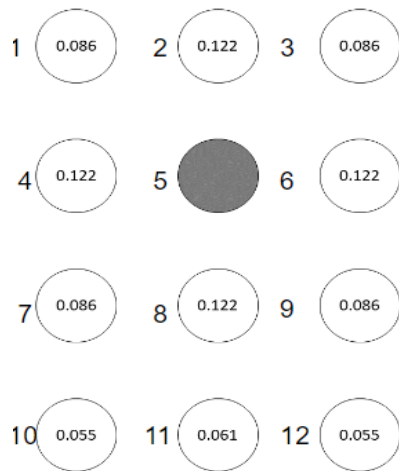


Figure 7: The experimental grid with pitfalls numbered from 1 to 12. Depending on the experimental set-up, the release point was located at number 5 or 8. The numbers inside the pitfalls indicate the chance that a recaptured beetle would fall in that certain trap. Some directions of dispersal can be considered the same. Therefore, pitfall 1 and 3, pitfall 4 and 6, pitfall 7 and 9, and pitfall 10 and 12 are grouped together.

The expected number of beetles recaptured for each pitfall (table 1) was calculated by multiplying the number of recaptured beetles in the experimental set-up with the chance that a recaptured beetle would fall in that certain trap (figure 7).

Table 2: The observed number of beetles recaptured in the study sites. RP= Release Point.

Release point	Pitfall 1+3	Pitfall 2	Pitfall 4+6	Pitfall 5	Pitfall 7+9	Pitfall 8	Pitfall 10+12	Pitfall 11
Wheat, Crop	2	6	2	RP	3	0	2	1
Wheat, Field strip	0	1	0	1	4	RP	4	1
Beet, Crop	6	1	7	RP	9	5	4	3
Beet, Field strip	0	1	1	0	8	RP	3	1

Some of the observed number of recaptured beetles per pitfall seem to differ from the expected number of recaptures predicted by the null model (table 1). These values are highlighted in green and red. Green indicates an observed value that is at least 1.5 times higher than expected and red indicates an observed value that is at least 0.5 times lower than expected.

Table 3: The probability that the observed pitfall recaptures were found, if the beetles would disperse according to the null model. These probabilities were calculated using the binomial distribution model. RP= Release Point.

Release point	Pitfall 1+3	Pitfall 2	Pitfall 4+6	Pitfall 5	Pitfall 7+9	Pitfall 8	Pitfall 10+12	Pitfall 11
Wheat, Crop	0,25	0,01	0,14	RP	0,24	0,13	0,28	0,38
Wheat, Field strip	0,28	0,36	0,13	0,37	0,16	RP	0,08	0,37
Beet, Crop	0,18	0,05	0,14	RP	0,07	0,18	0,21	0,20
Beet, Field strip	0,20	0,38	0,21	0,16	0,01	RP	0,23	0,32

To account for multiple independent tests (4 experiments with 7 modes of dispersal = 28), the alpha value needed to be adjusted. For this the Bonferroni Correction was used ($\alpha=0.00179$). None of the observed number of recaptured beetles per pitfall significantly differs from the number of beetles recaptured predicted by the null model (table 3).

Table 4: Observed number of recaptured beetles divided by the expected number of recaptured beetles.

Release point	Pitfall 1+3	Pitfall 2	Pitfall 4+6	Pitfall 5	Pitfall 7+9	Pitfall 8	Pitfall 10+12	Pitfall 11
Wheat, Crop	0,7	3,1	0,5	RP	1,1	0,0	1,1	1,0
Wheat, Field strip	0,0	1,5	0,0	0,7	1,5	RP	2,1	0,7
Beet, Crop	1,0	0,2	0,8	RP	1,5	1,2	1,1	1,4
Beet, Field strip	0,0	1,2	0,4	0,0	2,3	RP	1,2	0,6

Dispersal rates: theoretical null model

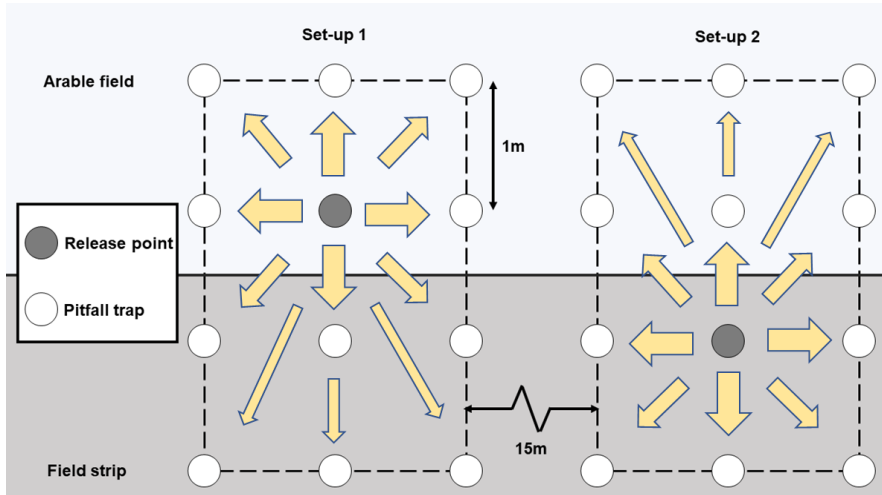


Figure 8: The expected dispersal rates of the recaptured beetles if the beetles would disperse according to the null model. The thickness of the arrows indicates the dispersion rate to a particular pitfall. The chances per pitfall can be found in figure 7.

The chance for a beetle to fall into a pitfall increases when the distance to the release point is lower (figure 8).

Dispersal rates: Observed in the winter wheat study site

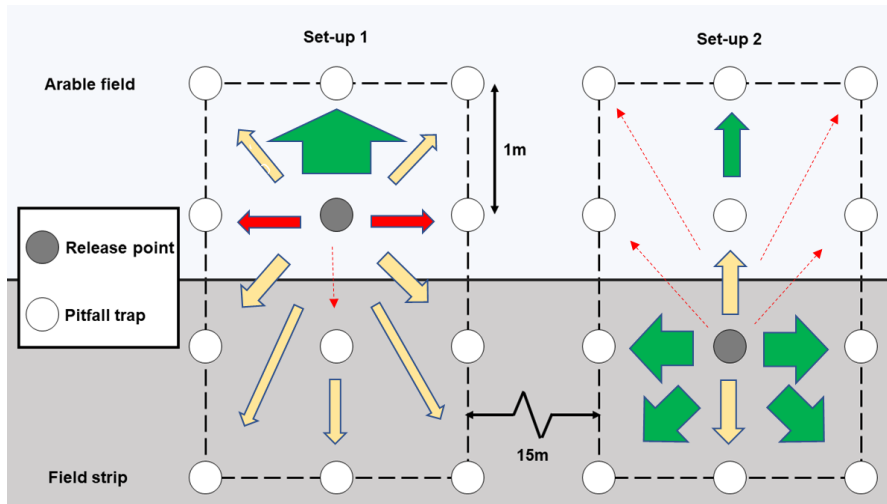


Figure 9: The observed dispersal rates of the recaptured beetles in the winter wheat study site. The ratio observed recaptured beetles:expected recaptured beetles (table 4) was used to modify the thickness of the arrows. The thickness of the arrows indicates the dispersion rate to a particular pitfall. A dotted line was used to point out that the number of recaptures was zero.

Compared to the null model, dispersion deeper into the crop field seems to be higher when released inside the crop field. Also, when released inside the field strip, dispersion within the field strip seems to be higher (figure 9).

Dispersal rates: observed in the sugar beet study site

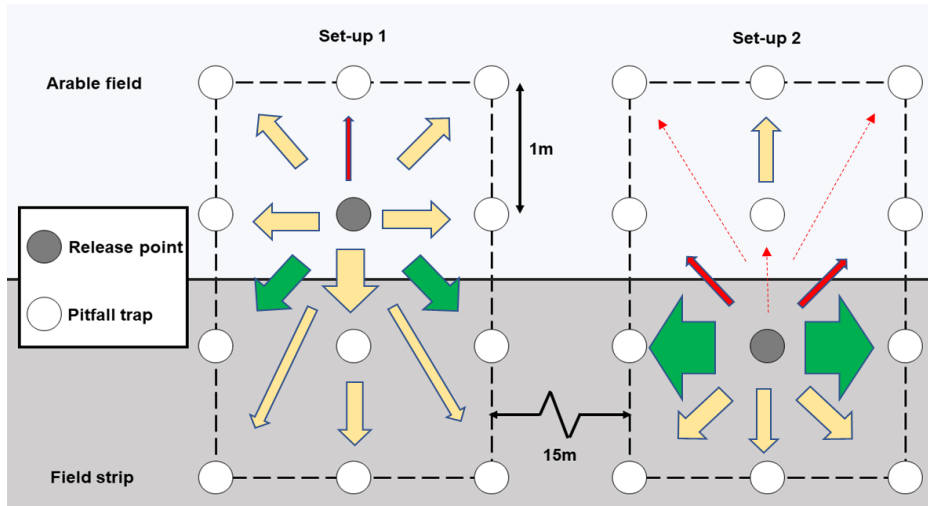


Figure 10: The observed dispersal rates of the recaptured beetles in the sugar beet study site. The ratio observed recaptured beetles:expected recaptured beetles (table 4) was used to modify the thickness of the arrows. The thickness of the arrows indicates the dispersion rate to a particular pitfall. A dotted line was used to point out that the number of recaptures was zero.

Compared to the null model, dispersion deeper into the crop field seems to be lower when released inside the crop field. Also, there seems to be more dispersion to the field strip. When released in the field strip, border crossing to the crop field seems to be lower than the null model predicts. Moreover, dispersion within the field strip seems to be higher (figure 10).

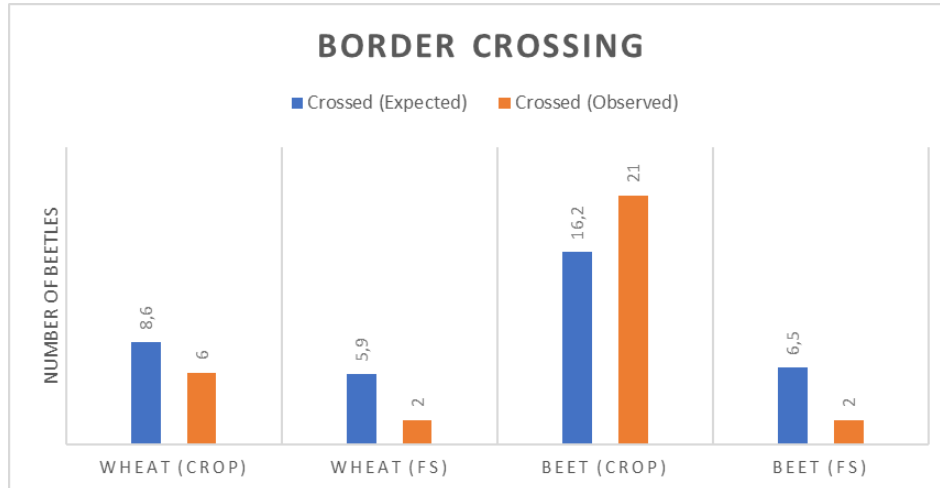


Figure 11: The number of recaptured beetles that were expected to cross the border if dispersion was according to the null model and the number of recaptured beetles that were observed to cross the border. The x-as indicates the study site (Wheat or Beet) and the release point (Crop or Field Strip (FS)).

When released inside the crop field in the winter wheat study site, there is no significant difference found between expected and observed border crossings ($p=0.48$). When released inside the field strip in the winter wheat study site, the observed border crossings seem to be lower than the expected border crossings. However, this result is not significant ($p=0.06$). When released inside the crop field in the beet study site, dispersion to the field strip seems to be higher than the null model predicts. Again, no significant difference was found ($p=0.1$). When released inside the field strip in the beet study site, there were significantly less border crossings to the beet field than the null model predicts ($p=0.02$).

Discussion

Carabidae are an important insect family for sustainable agriculture because of their abundance and their additive values to ecosystem services, with an emphasis on natural pest control. Woodcock et al. (2015) has demonstrated that carabidae in crop fields are present in higher numbers when adjacent to fieldstrips. However, dispersal mechanisms of carabidae are rather unexplored fields. Identifying mechanisms influencing carabidae dispersal can help farmers and policymakers make more thorough decisions on sustainable farming.

By capturing and releasing *P. melanarius* on fieldstrip-cropfield borders, surrounded by pitfall traps in grid-like structures we managed to observe a mechanism where the subject species have a higher tendency to disperse from crop field to field strip in beet fields compared to winter wheat fields. In winter wheat fields there is no real indication found that the border is perceived as a barrier since frequent border crossings are documented. Furthermore, in beet fields, when released in the field strip, few border crossings and many parallel movements are observed. Also, in beet fields, when released in the crop field, more border crossings are documented than expected. This suggests that in beet fields the border is perceived as a barrier only from the fieldstrip side and that habitat selection should also be taken into account.

Woodcock et al. (2008) found that beetle abundance can be partially explained by vegetation density and Turin (2000) indicated that *P. melanarius* abundance is low in poor open habitats, and rich in dense structures. These statements are in line with our findings that suggest that *P. melanarius* preferably moves to dense habitats. Based on this framework and our study we suggest that field strip-crop field borders can function as a barrier when the vegetation structures on the opposing side are not in line with the preference of *P. melanarius*. Also, certain habitats may function as an attractor when the opposing side is in line with their preference.

Although interesting data and conclusions are found, this study comes with a number of limitations. Firstly, after statistical analysis it appeared that the only significant result is that *P. melanarius* disperses less to the beet field compared to theoretical random dispersion. However, this p-value is a result of chi-square tests with a low sample size ($n=14$) and it is debatable whether this sample size is high enough for a valid chi-square test (Whitlock, 2014). Nevertheless, to test whether there was a significant difference in observed and expected border crossings, a chi-square test was performed four times. To conform to an overall $\alpha=0.05$ we had to adjust the α -value per individual test. According to the Bonferroni adjustment the α -value needed to be adjusted to $\alpha=0.0125$, and this makes all results insignificant. However, it is worthy to note that although the results are insignificant, we did find trends that are of promising character for future research and implications.

Secondly, to test whether *P. melanarius* disperse differently over the borders, the measurements are compared to a theoretical null model, which implies that *P. melanarius* disperses randomly. This implication however might not represent normal dispersal behavior of *P. melanarius*. A counterargument is that Bosma (2019) measured within habitat dispersion of *P. melanarius* and did not find a preference for dispersion in either beet or wheat fields. Although, Bosma did use a different setup compared to our experiments and might not be a suitable comparison. To make our findings more valuable it is of added value to implement control groups that measure dispersal of *P. melanarius* in set-ups located in field strips, and in both types of arable fields.

Lastly, this research was conducted between 9/5/22 and 20/5/22, all on one farm. This comes with a series of environmental factors that are not taken into account as possible explanations for the measured data. For instance, the time of year can have drastic effects on beetle dispersions. Also, weather conditions are not taken into account in the analysis, since there was not enough data to make valid comparisons. On most of the sampling days there was no precipitation and low groundwater levels. Consequently, the results only correspond to dry environments, and may be different when weather conditions are more wet. On the other hand, comparisons between experiments are still valid because they are conducted in the

same time period. Furthermore, P.H. Mulder has a rather unconventional way of farming and uses sustainable techniques to a certain extent. This makes Mulders farm an interesting, but not a model farm, and conclusions formed in this study may not be applicable to other farms.

This research should be considered as an exploratory study because the experiments are done on a local and short scale. We have shown that *P. melanarius* seems to disperse less to open (beet) fields than to dense (winter wheat) fields from set-aside fieldstrips. However, our statistical analysis does not hold much power and formulated conclusions must be considered specific and locally.

To increase the comprehension of ground beetle dispersion into arable fields we suggest expanding the research in a number of ways. 1) Increase sampling size by establishing more set-ups on the locations. 2) Increase the time frame of the measurements over the duration of the crop cultivation, to account for change in dispersion with respect to crop coverage/biomass increase. This comes with added measurements of the crop biomass/coverage over the same period of time. 3) Increase the number of years these experiments are executed to eliminate random annual factors. 4) Perform experiments over a series of farms to account for a series of uncontrollable factors, e.g. differences in farming methodologies, or soil- and fieldstrip species- compositions. 5) Increase the number of crops in the study, now only low (beet) and high (winter wheat) density crops are considered. However, dispersion in other vegetation types is of interest as well. 6) Integrate valid control groups instead of using theoretical random dispersal models.

In the study we found that in dense crop vegetation structures the border probably does not function as a barrier. But in open crop vegetation structures the border functions as a barrier from the field strip side, and may attract *P. melanarius* from the crop field side. The results imply that set-aside field strips may not be an effective solution to function as a source for ground beetles in sugar beet fields because dispersion into the crop field is low. However, we would like to appoint that this can result in a misconception, because the crop fields have open vegetation structures in May, shortly after sowing, but later in the season the crop coverage increases, thereby also increasing the dispersal into the crop field. Furthermore, Woodcock et al. (2005) already showed that ground beetles are present in higher numbers in crop fields connected to fieldstrips. This study shows that borders between fieldstrips and crop fields do influence ground beetle dispersal. However the borders should not only be perceived as barriers, but can also function as an attractor if the crop vegetation has an open structure

Over 40% of insect species are threatened with extinction (Sánchez-Bayo & Wyckhuys, 2019). As the main driver for this event is intensive agriculture, integrating farming with local ecosystems might be a measure that could counteract this decline to a certain extent. Implementing field strips on arable fields may be an effective measure to enhance insect biodiversity. These findings have provided a better understanding on the mechanisms behind the dispersal of carabidae among field strips and crop fields and could be of use for policy makers and farmers that intend to preserve biodiversity and increase natural pest control.

Reference List

- Albrecht, M., Duelli, P., Schmid, B., & Mueller, C. B. (2007). Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *Journal of Animal Ecology*, 76(5), 1015-1025
- Bosma, M., (2019). Arthropod abundance in agriculture. Quantifying abundance and activity of carabid beetles (Carabidae) in arable fields, University of Groningen.
- Fournier, E., & Loreau, M. (2002). Foraging activity of the carabid beetle *Pterostichus melanarius* Ill. in field margin habitats. *Agriculture, Ecosystems & Environment*, 89(3), 253–259. [https://doi.org/10.1016/S0167-8809\(01\)00216-X](https://doi.org/10.1016/S0167-8809(01)00216-X)
- Fraser, R.D.B. (1972). Keratins: Their composition, structure and biosynthesis. Bannerstone House: Charles C Thomas. pp. 3–6. ISBN 978-0-398-02283-9.
- Haaland, C., Naisbit, R. E., & BERSIER, L. F. (2011). Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity*, 4(1), 60-80.
- Hawthorne, A. J., M. Hassall, and N. W. Sotherton. 1998. Effects of cereal headland treatments on the abundance and movements of three species of carabid beetles. *Applied Soil Ecology* 9:417–422.
- Kromp, B., Hann, P., Kraus, P. & Meindl, P. (2004) Viennese Programme of Contracted Nature Conservation ‘Biotope Farmland’: monitoring of carabids in sown wildflower strips and adjacent fields. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie*, 14, 509–512.
- McCabe, E., G. Loeb, and H. Grab. 2017. Responses of Crop Pests and Natural Enemies to Wildflower Borders Depends on Functional Group. *Insects* 8:73.
- Norris, K.R. (1994) General biology. *Systematic and Applied Entomology: An Introduction* (ed. I.D. Naumann), pp. 68–108. Melbourne University Press, Carlton, Australia.
- Pe’er, G., Y. Zinggrebe, J. Hauck, S. Schindler, A. Dittrich, S. Zingg, T. Tschardtke, R. Oppermann, L. M. E. Sutcliffe, C. Sirami, J. Schmidt, C. Hoyer, C. Schleyer, and S. Lakner. 2017. Adding Some Green to the Greening: Improving the EU’s Ecological Focus Areas for Biodiversity and Farmers. *Conservation Letters* 10:517–530.
- Pfiffner, L., Luka, H., Jeanneret, P. & Schupbach, B. (2000) Effects of ecological compensation areas on the carabid fauna. *Agrarforschung*, 7, 212–217.
- Raven, P. H., & Wagner, D. L. (2021). Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences*, 118(2).
- Royal Netherlands meteorological institute (KNMI)
- Sánchez-Bayo, F., & Wyckhuys, K. A. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological conservation*, 232, 8-27.
- Smith, J., S. Potts, and P. Eggleton. 2008. The value of sown grass margins for enhancing soil macrofaunal biodiversity in arable systems. *Agriculture, Ecosystems & Environment* 127:119–125.
- Symondson, W. O. C., Sunderland, K. D., & Greenstone, M. H. (2002). Can generalist predators be effective biocontrol agents? *Annual review of entomology*, 47(1), 561-594.
- Turin, H. 2000. De Nederlandse loopkevers, verspreiding en oecologie (Coleoptera: Carabidae). *Nederlandse Fauna* 3: 1-666. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & European Invertebrate Survey-Nederland, Leiden.
- Tang, WJ; Fernandez, JG; Sohn, JJ; Amemiya, CT (2015). "Chitin is endogenously produced in vertebrates". *Curr Biol*. 25 (7): 897–900. doi:10.1016/j.cub.2015.01.058. PMC 4382437. PMID 25772447.
- Wageningen University. (2006). grondsoortenkaart [Map].
- Whitlock, M. C., & Schluter, D. (2014). *The Analysis of Biological Data*, Second Edition (2nd ed.). Roberts and Company Publishers.
- Wildschut, R. (2021). Set aside field strips for biodiversity conservation. University of Groningen.

- Woodcock, B. A., Potts, S. G., Westbury, D. B., Ramsay, A. J., Lambert, M., Harris, S. J., & Brown, V. K. (2007). The importance of sward architectural complexity in structuring predatory and phytophagous invertebrate assemblages. *Ecological Entomology*, 32(3), 302-311.
- Woodcock, B.A., Westbury, D.B., Tscheulin, T., Harrison-Cripps, J., Harris, S.J., Ramsey, A.J., Brown, V.K. & Potts, S.G. (2008) Effects of seed mixture and management on beetle assemblages of arable field margins. *Agriculture, Ecosystems & Environment*, 125, 246–254.
- Woodcock, B., Westbury, D., Potts, S., Harris, S., & Brown, V. (2005). Establishing field margins to promote beetle conservation in arable farms. *Agriculture, Ecosystems & Environment*, 107(2–3), 255–266. <https://doi.org/10.1016/j.agee.2004.10.029>