Short communication

Can δD and δ^{18}O stable isotopes be used to detect long-range dispersal among carabid beetles?

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ABSTRACT

We studied if hydrogen (δD) and oxygen (δ^{18}O) stable isotope values in three common carabid species in intensively managed agricultural landscapes in southernmost Sweden indicate long-range dispersal. We matched "emerging" (emergence tents) and "colonizing" (pitfall traps) individuals of three carabid species (*Trechus quadristriatus*, *Harpalus rufipes*, *Pterostichus melanarius*) to account for spatial and seasonal variability. There was higher dispersion of δD values among *H. rufipes* individuals as compared to values of the other two species, which suggests that *H. rufipes* individuals had the most variable spatial natal origin. The δD values were significantly lower among colonizing compared to emerging individuals in the flight capable and carnivorous species *T. quadristriatus*. This result suggests long-range migration of *T. quadristriatus* individuals from remote locations with deuterium depleted (lower δD) meteoric water. Our study provides a first effort towards understanding the δD and δ^{18}O dynamics in epigean carabids in northern European agroecosystems. Additional research on larger (preferably continental) spatial scales and experimental trials that attempt to disentangle major unaccounted sources of variation and decoupling of δD and δ^{18}O among carabids and other invertebrate natural enemies is urgently needed to allow a more frequent use of δD and δ^{18}O dynamics as indicators of long-range dispersal.

1. Introduction

Carabid beetles (Coleoptera: Carabidae) are important natural enemies of crop pests (Lang, 2003; Rusch et al., 2013) in many agroecosystems across Europe (Hendrickx et al., 2009), with several species being capable of long-range aerial dispersal (Chapman et al., 2005). To improve conservation biological control in agroecosystems, it is important to understand where invertebrate natural enemies, such as carabids, originate from and what their long-range movement potentials are. Such knowledge will simplify the management of their habitats through different life stages and at relevant scales. Long-range dispersal up to hundreds of kilometers by means of strong winds above the ground is considered as common for many insects (Drake and Gatehouse, 1995). While a widespread assumption has been that carabids in temperate regions do not frequently engage in this type of behavior, long-range aerial movements have been recorded for several carabid species (Chapman et al., 2005). In southern Sweden the abundant carabid species, *Trechus quadristriatus* (Schrank) and *Harpalus rufipes* (De Geer) are usually macropterous and have functional flight musculature, while the vast majority of *Pterostichus melanarius* (Illiger)

individuals are wingless in the region and thus lack flight ability (Hendrickx et al., 2009; Lindroth and Bangsholt, 1985). The small bodied *T. quadristriatus* has been observed dispersing over open water far away from the coast (Heydemann, 1967), while the larger *H. rufipes* is considered to be a good flier (Hendrickx et al., 2009) and has been collected from shore drift material suggesting dispersal over the sea water surface (Lindroth and Bangsholt, 1985). Thus, individuals of both these species can be expected to have better long-range dispersal capabilities than individuals of *P. melanarius*, which often are brachypterous. Although some carabid species are known to fly considerable distances, little is known about the contribution of long-range dispersal or local emergence to carabid population dynamics in intensively managed agricultural landscapes.

The ratio of heavier and lighter naturally occurring isotopes of hydrogen (δD) and of oxygen (δ^{18}O) in meteoric water (water derived from precipitation, e.g. lakes, rivers, most ground water) differ at regional to continental spatial scales (Bowen et al., 2005) and can in theory be used to establish the area of natal origin for long-range dispersing organisms (Brattström et al., 2008). δD and δ^{18}O values have been previously used in studies of vertebrate (Hobson et al., 2012) and

invertebrate (Hobson et al., 1999) long-range movement. Due to largely unknown metabolic processes, δD values of meteoric water are not directly transferable to values in animal tissue (Bowen et al., 2005). Instead these values tend to be higher in carnivorous vertebrates as compared to herbivorous and omnivorous species (Birchall et al., 2005). Insect herbivores, e.g. lepidopterans, tend to have higher δD values compared to their host plant (Peters et al., 2012). Both δD and δ^{18}O values strongly depend on global meteorological processes and e.g. temperature and elevation (Wassenaar, 2008). Although large-scale variation of δ^{18}O in meteoric water largely coincides with that of δD, δ^{18}O data is scarcely used for animal dispersal studies. The use of δ^{18}O values in combination with δD can potentially provide additional information concerning the dispersal ecology of species as oxygen can enter or exit animal tissue via more channels (air, water, and food) in biological dietary systems as compared to hydrogen (Wassenaar, 2008). Both values ideally can be used together in order to improve our understanding of dispersal in closely related taxa with different feeding preferences and dispersal modes.

Here we aim to explore causes of variation in δD and δ^{18}O values within and between three common carabid species in a temperate northern European agricultural region and discuss potential causal mechanisms. We captured carabids in an intensively managed agricultural area in southern Sweden, using emergence tents and pitfall traps. Carabid individuals captured in emergence tents likely spent their larval stage in the soils locally and emerged as adults during the crop growth season. Individuals captured in pitfall traps could have originated from remote locations before colonizing the sampling site. In this study we asked: (1) Is there a difference in δD and δ^{18}O values between locally emerging and colonizing carabid individuals? We hypothesized that there would be a higher probability of different isotopic composition, presumably caused by long-range dispersal, between emerging individuals as compared to colonizing ones for the two flight capable species *T. quadristriatus* and *H. rufipes*. No difference was expected for *P. melanarius*, as it is unlikely that a significant number of individuals of this species would be capable of long-range dispersal; (2) Do δD values of emerging and colonizing individuals depend on season? Assuming that most flight capable carabid species swarm at higher air temperatures (Kádár and Szentkirályi, 1998; Lindroth and Bangsholt, 1985), mass aerial dispersal events should mainly take place primarily in the peak of summer. This would increase the probability for differences in isotopic values later in the summer compared to spring when the average temperature is generally lower; (3) Among these polyphagous carabids, do primarily carnivorous species such as *P. melanarius* and *T. quadristriatus* have higher δD values compared to the omnivorous species *H. rufipes* (Purtauf et al., 2005; Ribera et al., 1999; Woodcock et al., 2010)? We expected that individuals of the more omnivorous species *H. rufipes* would have lower δD values than the other two primarily carnivorous species, as this species diet is largely based on plant matter. Finally, we also tested if δD and δ^{18}O values were correlated as δD and δ^{18}O values undergo a decoupling in food webs (Hobson and Koehler, 2015) from the meteoric relationship.

2. Materials and methods

The samples used in the present study comprised a subselection from a dataset generated by the sampling scheme described by Hanson et al. (2016). The three species mentioned in the introduction were handpicked for their differences in dispersal characteristics and feeding preferences, and because they were common enough to satisfy the design parameters for the present study (described below). Thus while the original full carabid species-assemblage dataset covered 66 sites distributed across 22 landscape locations (each with 1 spring-sown sugar beet site, 1 autumn-sown wheat site, and 1 ley site), only 12 out of these 66 sites had adequate abundance in both collection methods for any of the three selected species. Field work was carried out during April-August 2011 in a study area covering approximately 850 km^2

dominated by annually tilled farmland located in the province of Scania in southernmost Sweden. Emerging carabids were sampled with one emergence tent and colonizing individuals were sampled with three pitfall traps at each site (field). The tents, inserted into the soil to a depth of 10 cm with flaps around the base, had a base surface area of 0.6×0.6 m, a height of 0.6 m and a synthetic fabric with 16.7×5 mesh cm^{-2} (MegaView ScienceTM). A bottle at the top and a plastic cup (9 cm width $\times$ 6 cm depth, 250 ml) were used to collect carabids. Thus, the emergence tents captured individuals that were likely to have developed in the soil of the sampling site. Each pitfall trap consisted of a plastic cup, same type as used inside the tent, with a 15×15 cm metal sheet roof placed approximately 2 cm above the cup rim. As such, the pitfall traps captured individuals that "colonized" the sampling site either from within the same field, or from the surrounding landscape or, depending on long-range dispersal abilities, from far more remote locations. The pitfall traps inside and outside the tent were dug down into the soil so that the rim was at level with the soil surface. Bottles and pitfall traps were partially filled with 50–70% propylene glycol and a small amount of detergent. All traps were emptied fortnightly from the end of April until the beginning of August. Trap contents were transferred to ethanol (70%) for storage, which has been shown to not bias invertebrate δD or δ^{18}O (Myers et al., 2012). To the knowledge of the authors, no peer-reviewed publication has stated concerns for biased δD or δ^{18}O values after storage in propylene glycol. Captured carabids were determined to species according to Lindroth and Bangsholt (1985).

For each of the three selected species, we matched individuals in terms of co-occurrence of emerging and colonizing individuals at sampling sites and seasons (early and late). Early season individuals were collected between 2nd and 31st of May 2011 and late season individuals were collected between 11th of July and 8th of August 2011. Thus early and late season individuals were temporally separated by a minimum of 41 days. To be certain about the potential flight ability of all individuals in the analysis, we checked each individual that was used for stable isotope analysis for presence of wings. All *T. quadristriatus* and *H. rufipes* individuals were macropterous and all *P. melanarius* individuals in the analyses were brachypterous. As such, *T. quadristriatus* individuals emerging early (n = 8) and late (n = 11) in the season, and colonizing early (n = 10) and late (n = 12) in the season were collected from four sugar beet sites; *H. rufipes* individuals emerging early (n = 9) and late (n = 11) in the season, and colonizing early (n = 10) and late (n = 10) in the season were collected from three ley sites and one sugar beet site; and *P. melanarius* individuals emerging early (n = 11) and late (n = 12) in the season, and colonizing early (n = 12) and late (n = 12) in the season were collected from three ley sites and one winter wheat site. As all *T. quadristriatus* individuals had been collected from sugar beet sites, one could argue that crop related management, such as irrigation, could affect carabid δD and/or δ^{18}O values and therefore confound tests between species. Further, we detected significant correlations between δD values of emerging carabids and spatial coordinates, which potentially could have confounded the between-species analysis (Appendix A). However, a supplementary analysis did not reveal additional effects of cover type on carabid δD/δ^{18}O composition after accounting for spatial location (Appendix A), and by controlling for spatial coordinates and cover type in the between-species model, any variation caused by these factors were accounted for in the results.

The selected carabid individuals were dried at 60° C for 24 h and were immediately transferred to a desiccator where they were left to cool down to room temperature. For *T. quadristriatus* the whole beetles were used in the samples, as it otherwise would not have been possible to get enough biomass for the isotopic analysis. Dried individuals of *P. melanarius* and *H. rufipes* were ball milled and a subsample of the resulting powder was used. Each sample was weighed three times using a ± 10 µg scale, the mean value of these three measurements was used as the approximated weight for each sample of dried tissue. Stable