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Short communication

Positive density–distribution relationship in Finnish butterflies

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Species that are locally abundant tend to be more widespread than species that are locally rare. However, the opposite relationship has recently been observed with extensive abundance data for Finnish butterflies collected by voluntary lepidopterist. We were concerned about the suitability of these data for studying the distribution–abundance relationship in Finnish butterflies. Thus, we reviewed Finnish mark–recapture studies that report data for butterfly density. In these data, we found a positive density–distribution relationship for butterflies. Our study supports the conclusion that the positive distribution–abundance relationship is a general pattern for butterflies.

Introduction

A positive relationship between local density and distribution of species has been observed in a variety of species assemblages over a spectrum of spatial scales, and it has been suggested that it may be almost a universal pattern in ecology (Hanski *et al*. 1993, Lawton 1993, Gaston *et al*. 1997, Gaston & Blackburn 2000). In other words, species that are locally abundant tend to be more widespread than species that are locally scarce. Recently, this view has been questioned by Päivinen *et al*. (2005) and Komonen *et al*. (2009; *see* also Kotiaho *et al*. 2005), who observed a negative distribution–abundance relationship (Päivinen *et al*. 2005) by analyzing extensive data on the abundance of Finnish butterflies (NAFI, http://www.ekay.net/). Based on further analysis of the data, they suggested that positive distribution–abundance relationships might not be as general a macroecological pattern as previously thought (Komonen *et al*. 2009). Blackburn and Gaston (2009) presented criticism for the method to control for sampling effort used by Komonen *et al*. (2009, *see* also Kotiaho *et al*. 2009). Here we continue the criticism of the data and analyses used by Päivinen *et al*. (2005) and Komonen *et al*. (2009).

The NAFI data used by Päivinen *et al*. (2005) and Komonen *et al*. (2009) are based on observations of butterflies collected by voluntary lepidopterists in Finland. The NAFI database includes the number of butterfly individuals for each species observed in 10-km^2 squares covering the whole of Finland. Although robust guidelines on how to collect the data are provided (for example that not only rare species should be reported), these guidelines are not very specific. This creates biases in the database (Saarinen *et al*. 2003). For example, voluntary lepidopterists often are interested in observing rare species with known occurrence sites, thus making rare species overabundant in the database. Päivinen *et al*. (2005) and Komonen *et al*. (2009) controlled for this effect by dividing the mean local abundance by the number of observation days in their analysis. These data were correlated with the distribution data of Finnish butterflies (Huldén *et al*. 2000) to calculate the distribution-abundance relationship.

We believe that the correction made by Päivinen *et al*. (2005) and Komonen *et al*. (2009) for abundance in the NAFI database was not enough in controlling the possible effects of sampling of rare species with known occurrence sites. First, the high-density locations of common species are likely to be undersampled as compared with those of rare species. The reason is that voluntary lepidopterist may not be interested in locating an optimal habitat (with highest density) for common species, whereas known occurrence sites where rare species are observed are likely to be optimal habitat with the highest density for the species. In other words, common species are likely to be reported from areas where they occur in low or medium densities more often than rare species. This bias will not be corrected by dividing the abundance data by sampling days. Second, the density of butterflies in Finland typically peaks in the middle of the flight season and densities are lower at the beginning and at the end of the flight season. Rare species are likely to be sampled during the best season to observe these species, as voluntary lepidopterists may want to make their field trips to known locations of rare species (compare with twitching trips by bird watchers to watch a rare species) when the likelihood of encountering these species is high. Instead, common species may be observed more evenly throughout the flight season of the species. Finally, to our knowledge the number of observation days in the most intensively monitored grid squares could become very high in the NAFI database. The intensively monitored grid squares could, for example, surround the observers' home or summer residence. It seems likely that in these sites common species are overabundant compared to rare species. Thus, in some cases the number of observation days used to divide local abundance (Päivinen *et al*. 2005, Komonen *et al*. 2009) may have been very large for common species. In contrast, for rare species the number of observations days is likely to be low, as the known occurrence sites of the latter are often visited only on one or a few days. Consequently, it is questionable whether dividing the mean local abundance by the number of observation days [the method used by Päivinen *et al*. (2005) and Komonen *et al*. (2009)] treated the density of common and rare species similarly. The above-mentioned effects will bias density estimates by increasing the abundance of rare species in the NAFI data.

Due to the above-mentioned concerns about the suitability of NAFI data for distribution-abundance studies, we performed a review on Finnish butterfly studies that used mark–recapture methods to calculate population size (Helos 2008). We correlated the local densities in these studies with the distributions of these species using data of Huldén *et al*. (2000).

Material and methods

All mark–recapture studies of Finnish butterflies that reported population size estimates and sizes of sampling areas were included in this review and were used to calculate local density of the species (Table 1). Studies were found by searching Web of Science and by asking butterfly researchers at Finnish universities and environmental agencies whether they knew of any published mark–recapture studies performed at their institute (for more information, *see* Helos 2008).

Results and discussion

The reviewed mark–recapture data showed a clear positive density–distribution relationship for Finnish butterflies (Fig 1; Spearman rank correlation: $n = 15$, $r_s = 0.56$, $p = 0.03$). Naturally, there are possible sources of error in the reviewed density estimates. The studies, for example, originate from different years and methods used to calculate population size varied. In addition, Päivinen *et al*. (2005) and Komonen *et al*. (2009) estimated abundance across Finland, whereas we used local abundance, although we do not see any reason to expect

Table 1. Mark-recapture studies used in the distribution-abundance analysis of Finnish butterflies.

Species	Distribution index[a]	Study location	Size of study area (ha)[b]	Estimated population size	Density (inv. ha^{-1})	Reference
Aphantopus hyperantus	624	Lammi and Joutseno	9.2 and [c]	5286 and 9399	1250[d]	Helos 2008, Valtonen & Saarinen 2005
Boloria aquilonaris	328	Lammi	19	2603	137	Helos 2008
Boloria euphrosyne	734	Ruokolahti	4.7	768	163	Blomqvist *et al.* 2003
Boloria titania	22	Pernaja	6.1	300	49	Kuussaari 1999
Euphydryas aurinia	22	Joutseno/ Imatra	21.4	912	43	Klemetti & Wahlberg 1997
Euphydryas maturna	217	Joutseno	6.1	1126	185	Selonen 1997
Melitaea cinxia	26	Åland	20.7	10025	484	Hanski *et al.* 1994
Melitaea diamina	12	Orivesi	21.4	2198	103	Wahlberg *et al.* 1996
Melitaea athalia	468	Joutseno	21.6	7208	334	Selonen 1997
Parnassius apollo	35	SW Finland	51.3	413	8	Fred & Brommer 2003, Fred *et al.* 2006
Parnassius mnemosyne	31	Rauma	6.2 and 7	1700 and 1000	209[d]	Välimäki *et al.* 2000, Välimäki & Itämies 2003
Pararge achine	27	Hämeenlinna	2.7	720	267	Laitala 1997
Glaucopsyche arion	25	Liperi	5	310	62	Pajari 2002
Scolitantides orion	24	Lohja	0.4	62	155	Saarinen 1993
Scolitantides vicrama	4	Säkylä	18.1	861	48	Väisänen *et al.* 1994

[a] Distribution index based on Huldén *et al.* (2000), [b] only preferred habitat of the species included, [c] Missing, density calculated by original authors, [d] mean of two studies.

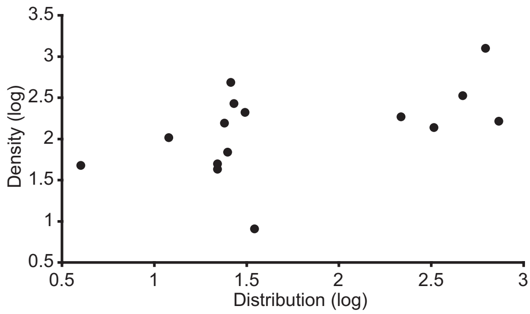

Fig. 1. Local density in mark–recapture studies *vs.* nation–level distribution of Finnish butterflies.

that this would affect our conclusions. The sites of mark–recapture studies also likely are not a random sample of sites where the species are present. This is particularly the case for the mark–recapture studies of rare species, as these studies are usually located in places with the highest density for the species. This effect may increase the density of rare species as compared with the density of common species in our data (a similar bias to what we expect in the NAFI data, *see* Introduction). In any case, this possible bias (possibly leading to a false negative distribution–abundance relationship) did not prevent us from observing a positive distribution–abundance relationship. In addition, the point made by Komonen *et al*. (2009) that the positive distribution–abundance relationship may be due to missing rare species should not have an effect here, because mark–recapture studies tend to be focused on rare species (9 of the 15 studied species are classified as vulnerable or endangered in Finland).

Our observed positive density–distribution relationship with mark–recapture data of Finnish butterflies supports our concern (*see* Introduction) that NAFI data are not suitable for studying distribution–abundance relationships. Our results support the conclusion that a positive distribution–abundance relationship in butterflies (Cowley *et al*. 2001) is as general a trend as it was before the work by Päivinen *et al*. (2005) and Komonen *et al*. (2009).

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