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Subtle Effects of Experimental Grassland Fragmentation on Density, Species Composition and Functional Dispersion of Gastropods

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Abstract: The fragmentation of continuous habitats has significant consequences for species and for the functional diversity of plant and animal communities. Fragmentation effects can be indirect, can occur at different spatial scales and may vary over years. Small fragmentation-related effects may only be detected in standardized, controlled field experiments accounting for the natural variation in environmental conditions and in remnants of habitat. Using a non-invasive trapping approach, we examined the responses of terrestrial gastropods (snails and slugs) to small-scale habitat fragmentation in a controlled experiment conducted in three species-rich, nutrient-poor calcareous grasslands in the Jura Mountains, Switzerland, over four years. We found site-specific differences in species richness, individual density, and species composition. Experimental grassland fragmentation did not significantly affect species richness or density, but affected functional dispersion (a measure of functional diversity) in the final year, indicating that fragmentation-related changes may occur with a time delay. Similarly, experimental fragmentation influenced the mean shell size of the snail assemblage and the proportions of individuals with certain life-history traits or habitat preferences in some years. The observed fragmentation effects were subtle and varied over time, underlining the importance of controlled field experiments.

Keywords: biodiversity; body size; functional diversity; habitat fragmentation; habitat preference; invertebrates; slugs; snails; species composition; terrestrial gastropods

1. Introduction

Habitat fragmentation is generally considered to be one of the major threats to biodiversity [1–3]. Fragmentation reduces the total area of original habitat, alters environmental conditions in remnants, creates isolated subpopulations, and interrupts the exchange of individuals and genes among populations [4–6]. The response of plant and animal species depends on their dispersal ability and life history, the type and size of the fragments, and the permeability of the matrix [7,8]. Habitat fragmentation occurs at different spatial scales. It ranges from small breaks in otherwise homogenous habitat to widely scattered fragments in a hostile matrix [9]. For each species, the relevant spatial scale is different depending on their resource needs and mobility [10,11].

In our study, we focus on semi-natural grasslands, which have been recognized as regional biodiversity hotspots in Europe [12,13]. As human-made habitats, dry, nutrient-poor calcareous grasslands harbour numerous species whose original habitats (peatlands, floodplains and rocky outcrops) have been largely destroyed [14]. However, semi-natural grasslands are fragile because their maintenance depends on traditional farming techniques [15]. During the past decades, increasing pressure for higher production at low costs has led to either an intensification of grassland use (increased stocking rate and/or

increased use of fertilizer) or to abandonment [16,17]. These two processes have led to a reduction in the area of semi-natural grassland [18]. The remaining fragments of the grasslands are frequently surrounded by intensively managed farmland and/or forest. Thus, nowadays, these grasslands are rare and fragmented, with the remnants differing in species composition [14,19]. Because of the among-site variation, it is difficult to derive general findings on the impact of further habitat fragmentation. Standardized field experiments in multiple remnant grasslands are a possible way to circumvent this problem [20].

We used terrestrial gastropods (snails and slugs) as a model group to investigate changes in species diversity, species composition and functional diversity in response to small-scale grassland fragmentation. Our study was conducted in the fourth to seventh years of a controlled fragmentation experiment in three nutrient-poor dry grasslands in the Swiss Jura mountains [21,22]. We mimicked grassland fragmentation through frequent mowing of the surrounding matrix over seven years, resulting in fragments of different sizes, separated from continuous high-turf grassland by a minimum distance corresponding to a local road. Because fragmentation effects frequently occur with a time lag [23–25], we started our study three years after the initiation of the experiment.

Terrestrial gastropods have limited mobility [26]. Because of their vulnerability to desiccation, even relatively short distances over exposed ground, as represented by the width of a country road, may lead to the partial isolation of populations [27,28]. Terrestrial gastropods are important decomposers [29,30] and are especially sensitive to land-use changes [31,32]. In dry grasslands, the majority of gastropod species have a life cycle of 1 year or even shorter [33], indicating that the local assemblages had time to respond to the experimental fragmentation and the consequent changes in local environmental conditions. To minimize any disturbance of the gastropod communities, we used a non-invasive survey method, leaving individuals in place.

In our study, we firstly examined whether species richness, individual density and species composition of gastropods (snails and slugs combined) or snails only (shelled gastropods) were differently affected by the experimental fragmentation. We expected that species richness would decrease in fragments, and that the species composition of local assemblages in fragments would differ from that of control plots in continuous vegetation. The impact of fragmentation frequently develops over time [23,24,34]. Therefore, we expected fragmentation effects to become more apparent over time, as local populations of no-longer well-adapted species decline, while populations of other species benefit from the changed conditions. The results of this long-term fragmentation experiment showed increased plant biomass in fragments, mainly due to an edge effect [35]. Plant biomass is an important resource for gastropods [36]. In our experiment, plant biomass also retains humidity and affects temperature at the micro-scale [21]. We therefore expected an increase in gastropod individual density in fragments and a generally positive relationship between gastropod density and plant biomass. The species' responses to fragmentation may depend on their morphological and life-history traits. Therefore, we expected that the local gastropod assemblages in fragments would harbour species that, on average, differ in their traits from those in control plots. As a consequence, the functional diversity of the assemblages in fragments was also expected to be different from that in control plots. Furthermore, we examined whether local assemblages in fragments differ regarding specific traits such as snail shell size (a proxy for body size), age at sexual maturity and longevity (two measures related to generation length), and preferences for environmental conditions, which could explain different responses among species. Body size has previously been found to be important in fragmentation studies [37,38]. Body size is generally positively related to dispersal ability and, thus, to habitat size and fragment isolation [37,39]. Life-history theory predicts that age at sexual maturity decreases in harsh and less predictable environments [40]. In our study, fragments had larger temperature fluctuations than control plots, especially in the edge zones [21]. Therefore, we expected a higher proportion of gastropods with short generation lengths in fragments than in control plots. A change in environmental conditions may render a habitat less suitable for specialists of that habitat [41].

Conversely, species with a wide niche breadth might not be negatively affected by the relatively mild fragmentation. Thus, we expected the proportion of individuals belonging to habitat-generalist species, compared to those belonging to openland specialists, to be higher in fragments than in control plots. Because plant biomass was higher in fragments than in control plots [35], we expected a larger proportion of individuals belonging to species that prefer moist conditions to be in fragments than in control plots.

2. Materials and Methods

2.1. Study Sites

We conducted the experiment in three semi-natural, nutrient-poor calcareous grasslands in the Jura Mountains, Switzerland: Movelier (midpoint of site: 47.413558° N, 7.323867° E, 770 m a.s.l.; see inset air photograph in Figure 1), Nenzlingen (47.448586° N, 7.567864° E, 510 m a.s.l.), and Vicques (47.363867° N, 7.426114° E, 590 m a.s.l.). The grassland near Movelier was situated on a SSE-facing slope with an inclination of 20–22°, the one in Nenzlingen on a SW-facing slope (19–22° inclination), and the one in Vicques on a SE-facing slope (15–27°). The three grasslands belong to the TeucrioMesobrometum association, and were previously used as pasture for centuries [42,43]. For the fragmentation experiment, we rented c. 1.5 ha of grassland at each site and took over their management for 7 years in agreement with the owners. We fenced the rented areas and only mowed them at the end of the growing season in each year to prevent encroaching by woody plants. Compared to Movelier, soil depth was shallow in Nenzlingen and Vicques, with the bedrock exposed in several places, resulting in drier conditions. Mixed deciduous forest bordered all three sites. The distances among sites ranged from 9.5 to 18.8 km. Mean annual temperatures for the sites ranged from 7.4 to 8.9 °C, and precipitation from 917 to 1104 mm (long-term climate data derived from the WorldClim database [44], which fit well with locally measured data in Nenzlingen [21]). Annual precipitation during the study, at a nearby weather station in Laufen, was 963.8 mm in 1996, 898.6 mm in 1997, 1034.5 mm in 1998 and 1417.0 mm in 1999 (data obtained from MeteoSwiss [45]). The sites are described in detail in Baur et al. [14].

2.2. Fragmentation Experiment

We created experimental fragments in formerly continuous grassland by mowing the area surrounding them in 1993 (Figure 1). We then maintained this kind of fragmentation over seven years by frequently mowing the matrix around the fragments (7–11 times per year) throughout the growing season. The sward height of the matrix was held at a 4–5 cm height. The cuttings from the mowing were removed. We used a block design in which fragments were isolated by 5 m from the nearest unmown grassland and from other fragments, a distance representative of the width of the typical road in this region. In a mirrored design, we marked corresponding control plots 5 m from the same edge within the continuous undisturbed habitat (Figure 1). Each block contained fragments of three different sizes, separated by 5 m of mown matrix—one large fragment measuring 4.5 m × 4.5 m, one small fragment (1.5 m × 1.5 m), and two tiny fragments (0.5 m × 0.5 m)—and their corresponding control plots (Figure 1). However, small and tiny fragments and control plots were not considered in the present study, as there were few gastropods in them. The position of the fragment–control-plot pairs within a block were randomized. Three blocks were located in Movelier, five in Nenzlingen and four in Vicques. Thus, we had an overall sample size of 12 large fragments with 12 corresponding control plots. Within a study site, the distances between the nearest edges of blocks ranged from 25 to 135 m. Further details on the experimental design can be found in Zschokke et al. [21].
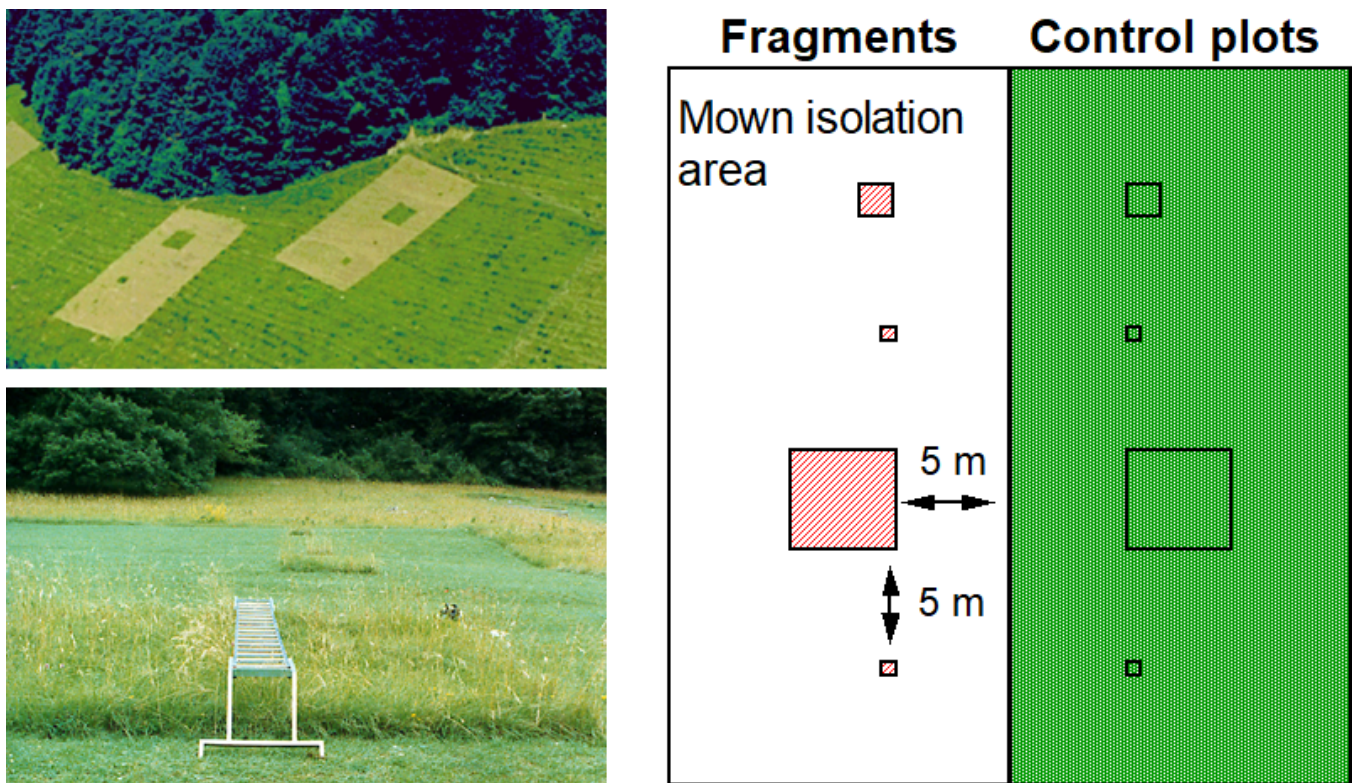
Figure 1. Experimental design. Starting in 1993, three semi-natural, dry, calcareous grasslands in the Jura mountains (Switzerland) were experimentally fragmented by regular mowing around the fragments. Twelve experimental blocks (29 m × 32 m) contained one large (4.5 m × 4.5 m), one small (1.5 m × 1.5 m) and two tiny (0.5 m × 0.5 m) fragments each, as well as corresponding control plots in unmown vegetation. The order of the fragment and control plot pairs within a block was randomized. Cardboard sheets (10 cm × 10 cm) were placed in the vegetation of large fragments and large control plots, close to the ground during rainy autumn nights, in the years 1996–1999. The cardboard sheets were arranged in a regular grid with 9 × 9 cardboard sheets. Small and tiny plots were not considered in this study. Photos: Study site Movelier from air (M. Wurtz); fragments in Nenzlingen with mobile working platform (B. Braschler).

2.3. Non-Invasive Gastropod Surveys

To assess gastropod diversity, we used cardboard trapping, a non-invasive method [46]. One survey was conducted each year in 1996−1999, in autumn (the 4th to 7th years after initiation of the experimental fragmentation). On each occasion, wet cardboard sheets were placed close to the ground in the vegetation, overnight, in rainy weather. These cardboard traps attracted terrestrial gastropods (snails and slugs) from below and from their close surroundings (up to 20 cm) [46]. The following morning, living gastropods attached to the sheets were identified in situ and, thereafter, released at the same spot. We placed the cardboard sheets (10 cm × 10 cm) in a grid of a 0.5 m × 0.5 m mesh size within each plot. Thus, we used 81 cardboard sheets per sample in each fragment and each control plot, or 1944 sheets per year in all blocks combined.

Individuals were identified at the species level. When necessary, specimens were brought to the lab for closer examination (few cases) and returned to the same plot the following day. For gastropod identification, we used the key by Kerney et al. [47]. The analyses were conducted at two different taxonomical levels: all gastropods (snails and slugs combined) and snails only. Snails are shelled gastropods, while slugs do not possess a visible shell [47]. The abundances of all species per experimental plot for each year are presented in Tables S1−S4.

We compared our survey data with existing species lists, based on data from surveys using different sampling methods (pitfall traps in 1993 [14] and 1999 [22], and visual search in 1994–1996 [48]) in the same study sites. With the exception of a few, mainly forest species, all gastropods recorded using other sampling methods were also found on the cardboard traps, confirming the sampling method comparison of Oggier et al. [46].

2.4. Functional Dispersion, and Morphological and Life-History Traits

As a measure of functional diversity, we considered functional dispersion (FDis). FDis is a measure of functional richness, which considers the species' relative abundances by estimating their dispersion in a multi-dimensional trait space [49]. FDis has no upper limit, and high values correspond to large numbers of different species. It can be computed if at least one species is present, in which case, FDis is zero. To calculate FDis we used life-history (age at maturity, longevity) and morphological (body size) traits of the species recorded in the plots. Age at sexual maturity had an ordinal scale (<1 year; 1 year; >1 year) as did longevity (<1 year; 1−2 years; >2 years). Data were retrieved from Falkner et al. [33], Bengtsson and Baur [50], and Baur [51]. Body size is expressed in a different way in snails and slugs. In snails, the mean shell size was considered (the larger of mean shell height or width); in slugs the mean extended body length was measured. To combine the measures of body size of snails and slugs for analyses of FDis, we used standardized values by expressing size as a proportion of the largest snail or slug species, respectively. The trait values used for each species are given in Table S5.

The traits considered in the calculation of FDis are all also likely to affect the response to the experimental fragmentation and how quickly it becomes visible. Therefore, we also examined the effects of fragmentation on snail traits separately (body size, age at maturity and longevity).

2.5. Habitat Preference

We considered two aspects of habitat preference in gastropods (Table S5): first, information on broad habitat preferences (openland specialist, forest specialist or habitat generalist occurring in openland and forest) was available for all species from Falkner et al. [33] and Kerney et al. [47]; second, information on humidity preference (ordinal scale: wet, moist and dry conditions) was compiled from Falkner et al. [33].

2.6. Plant Biomass

We used above-ground plant biomass of the preceding year as a measure of the productivity of the fragments and control plots, which may affect gastropod densities, species richness, FDis and body size. As most gastropod individuals in the plots examined belonged to species with an age at sexual maturity of 1 year or less, plant biomass of the preceding year reflected the environmental conditions under which they grew. Variation in plant biomass may affect environmental conditions in ways that filter for species with certain traits (e.g., smaller or larger body size) or habitat preferences, and thus, affect species composition. Dolt et al. [35] clipped all plants 5 cm above ground level (to preserve rosettes) between 6 and 15 October in 1996−1998 (plant biomass was not assessed in 1995, preventing the use of plant biomass in models on gastropod density, species richness and FDis for 1996). In each fragment and control plot, 20 subsamples covering 0.25 m^2 were randomly chosen [35]). Care was taken to ensure correct representation of edge and core samples in the plots. The plant samples were oven-dried (60 °C for 2 days and 80 °C for 2 h) and then weighed. Data on mean plant biomass for each experimental plot in 1996−1998 are given in Table S6.

2.7. Statistical Analyses

Statistical analyses were performed in *R* (ver. 4.1.1 [52]). We used observed species richness (hereafter species richness) as a surrogate for total species richness. Additionally, we performed individual-based rarefaction at the site level (for each year separately, and

for data from all years combined) to compare species richness among sites with different gastropod densities (function *rarefy* in package *vegan* [53]).

We used repeated measures ANOVA models to analyse whether relative density of gastropods or snails (expressed as number of individuals per cardboard trap) were affected by experimental fragmentation and the year of the survey, including the interaction. Post-hoc paired t-tests were conducted to explore the years among which gastropod or snail densities differed. As a second approach, we used linear mixed models to examine the effect of the experimental fragmentation on gastropod or snail density in separate years. In these models, fragmentation treatment (fragment or control plot) was entered as a fixed factor. Study site (Movelier, Nenzlingen or Vicques) and block nested in study site were entered as random factors. In a further approach, we included plant biomass (of the preceding year) as a covariate in these models, because gastropods and snails are expected to be influenced by plant biomass through increased productivity and changed moisture conditions [21,35]. The inclusion of plant biomass at a later stage was necessary because no data on plant biomass were available for 1995. This analysis was, therefore, restricted to three years. The vast majority of gastropod species recorded in our study attain sexual maturity within one year [33]. Hence, the environmental conditions of the preceding year (for which we used plant biomass as a surrogate) might be of crucial importance for the population dynamics of these species.

We used the same approaches as for relative density to analyse the effects of experimental fragmentation, year, and plant biomass of the preceding year on species richness of gastropods and snails. Species composition of fragments and control plots was analysed using permutational analysis of variance (PERMANOVA; function *adonis* in the package *vegan* [53]) and visualized using non-metric multidimensional scaling (nMDS; function *metaMDS* in package *vegan* [53]).

FDis of gastropods and snails in experimental plots was calculated using the function *dbFD* in package *FD* [54]. FDis was based on abundance data rather than presence/absence data and was, thus, more strongly influenced by abundant species than rare species. Abundant species may be more reflective of the environmental conditions than rare species. While some species typical of a habitat type are naturally rare, others may be rare as they are specialists from other habitat types represented by vagrants (e.g., forest specialists from the adjacent forest in the grassland). To analyse the effects of the experimental fragmentation on FDis of gastropods and snails, we used the same models and approaches as described for relative density and species richness.

For the analyses of body size, we considered only snails and used the actual shell size in mm rather than the standardized values used to calculate FDis. We calculated mean shell size of all snail species (weighted by their abundance) for each large plot in each year (hereafter, mean shell size of the snail assemblage). We used the same models and approaches as for FDis to examine the effects of year, experimental fragmentation, and plant biomass of the preceding year on mean shell size of the snail assemblage.

To analyse the effect of experimental fragmentation on age at sexual maturity, we used two classes (<1 year and 1 year combined, and >1 year). We examined whether the proportions of individuals belonging to these two age classes differ between fragments and control plots using Fisher's exact test for gastropod and snail assemblages in each year, separately. We used the same approach with Fisher's exact test to examine a possible effect on the proportion of individuals belonging to two longevity classes (<1 year and 1−2 years combined, and >2 years).

To examine whether the experimental habitat fragmentation affected the proportion of individuals belonging to habitat-generalist species in relation to those belonging to openland-specialist species, we conducted Fisher's exact tests for the gastropod and snail assemblages in experimental plots in each year. Similarly, we tested whether fragmentation influenced the proportion of gastropod and snail individuals showing different humidity preferences (three groups: wet, moist and dry) using Fisher's exact tests.

3. Results

3.1. Relative Density and Species Richness

Over the four years combined, we recorded 1726 snail and 2490 slug individuals belonging to 14 and 5 species, respectively, in the fragments and control plots combined. Relative density of all gastropods (number of individuals recorded per cardboard trap) did not differ among sites to the same degree as rarefied species richness (Table 1). However, Movelier had higher relative snail densities than the other two sites (Table 1a). Considering single years, both the relative density and rarefied species richness of gastropods increased over time, with the increase most pronounced in the final year of the study (Table 1). Overall, Vicques had lower observed and rarefied gastropod species richness than the other two sites, despite similar relative density (Table 1).

Table 1. Abundance (with relative density in brackets) and species richness (with rarefied species richness in brackets) of all gastropods and snails only at the three grassland sites for four years. Cumulative abundance and overall species richness combines the number of all individuals and all species, respectively, observed over four years.

(a) Abundance [1] (Relative Density) [2]	1996	1997	1998	1999	Cumulative Abundance
All gastropods					
Movelier [2]	212 (0.44)	99 (0.20)	201 (0.41)	498 (1.02)	1010 (0.52)
Nenzlingen [2]	252 (0.31)	305 (0.38)	374 (0.46)	946 (1.17)	1877 (0.58)
Vicques [2]	101 (0.16)	169 (0.26)	259 (0.40)	800 (1.23)	1329 (0.51)
Snails					
Movelier [2]	176 (0.36)	73 (0.15)	140 (0.29)	252 (0.52)	641 (0.33)
Nenzlingen [2]	99 (0.12)	64 (0.08)	94 (0.12)	292 (0.36)	549 (0.17)
Vicques [2]	81 (0.13)	123 (0.19)	136 (0.21)	196 (0.30)	536 (0.21)
(b) Species Richness (Rarefied Species Richness) [3]	1996	1997	1998	1999	Overall Species Richn
All gastropods					
Movelier [2]	9 (8.1)	10 (10.0)	10 (10.0)	11 (11.0)	15 (15.0)
Nenzlingen [2]	8 (6.8)	10 (8.3)	9 (8.3)	12 (10.6)	14 (14.8)
Vicques [2]	7 (7.0)	8 (7.4)	8 (8.0)	9 (8.2)	10 (10.0)
Snails					
Movelier [2]	7 (6.4)	8 (7.8)	9 (7.7)	9 (8.5)	12 (11.8)
Nenzlingen [2]	5 (5.0)	7 (7.0)	5 (5.0)	8 (7.3)	9 (9.0)
Vicques [2]	5 (5.0)	7 (6.2)	6 (6.0)	7 (7.0)	7 (7.0)

[1] Number of experimental blocks differed between sites. Therefore, 486 cardboard traps were set per year in Movelier, 810 in Nenzlingen and 648 in Vicques; [2] relative density is calculated as number of all gastropods or of snails only per cardboard trap, correcting for a few traps displaced by strong wind in 1997; [3] species richness calculated using individual-based rarefaction.

3.2. Effect of Experimental Grassland Fragmentation

Using an overall ANOVA model with repeated measures to incorporate the four years of the survey, we found no effect of the experimental fragmentation on the relative density of either gastropods or snails (number of individuals per cardboard trap) (Table S7). However, the relative density of both gastropods and snails differed significantly over the years. The relative densities were slightly higher in 1998 (only gastropods) and significantly higher in 1999 (both gastropods and snails) than in the preceding years (Table S8).

Analysing the data for each year separately, the experimental grassland fragmentation had no significant effect on the relative density of gastropods (Table 2a). When only snails are considered, there was a weak non-significant trend for higher relative density in control plots than in fragments in the final year (1999; Table 2b).

Table 2. Effects of experimental fragmentation on the relative density [1] of all gastropods (snails and slugs combined) or of snails only, in the years 1996–1999.

	1996			1997			1998			1999		
(a) All gastropods	df	F	*p*	df	F	*p*	df	F	*p*	df	F	*p*
Fragmentation treatment	1,11	2.51	0.14	1,11	1.29	0.28	1,11	0.12	0.74	1,11	2.54	0.14
(b) Snails												
Fragmentation treatment	1,11	0.87	0.37	1,11	1.01	0.24	1,11	0.53	0.48	1,11	3.62	0.083

[1] Relative density was calculated as number of individuals per cardboard trap and was log (x + 1)-transformed for analysis.

Gastropod abundance in grasslands may at least partly depend on plant biomass (providing shade and food and retaining humidity). In our field experiment, plant biomass ranged from 32.62 to 101.04 g dry weight per 0.25 m^2 among experimental plots in the three years examined. Plant biomass was higher in fragments than in the corresponding control plots in 1996 and 1998 (Table S9). Extending the LME models by including the plant biomass of the preceding year did not change the findings (Table S10). Plant biomass itself did not significantly influence the density of all gastropods in any of the years examined (Table S10). However, snail density in 1998 was influenced by plant biomass (Table S10). Snail density tended to decrease with increasing plant biomass in the preceding year ($R = 0.37$, $t_{22} = 1.84$, $p = 0.079$).

The observed species richness of both gastropods and snails did not differ between fragments and control plots using repeated measures ANOVAs (Table S11). However, the species richness of all gastropods and of snails only was higher in the final year of the study than the other years (Table S12). Analysing the data for each year separately, snail species richness tended to be lower in fragments in the final year of the study (Tables S13 and S14). If the plant biomass of the preceding year is included in the model, then snail species richness was significantly affected by plant biomass in the final year of the study (1999) and tended to be affected in 1998 (Table S14). In both cases, snail species richness decreased with increasing plant biomass in the preceding year.

3.3. Effect on Species Composition

Non-metric multidimensional scaling (nMDS) plots showed that the species composition of all gastropods differed among sites in three of the four years (Figure 2). This finding was confirmed by PERMANOVA (statistics shown on top of panels in Figure 2). However, the species composition of all gastropods was not influenced by experimental grassland fragmentation in any year. Considering snails only, nMDS plots indicated that species composition differed among sites in 1996 and 1999 (Figure S1).

3.4. Functional Dispersion (FDis)

The FDis (a measure of functional diversity) of snails only was significantly affected by fragmentation in the final year of our experiment (1999; Table 3). Using a repeated measures ANOVA combining data from all years, the fragmentation effect remained only as a weak tendency ($p = 0.084$; Table S15). Considering all gastropods, no fragmentation effect was found in any year (Table 3). Applying a repeated measures ANOVA, the FDis of all gastropods differed significantly over the years (Table S15), mainly due to the high FDis in 1996 compared to the following years (Table S16). In snails only, the repeated measures ANOVA revealed no differences in FDis over the years (Table S15). Including the plant biomass of the preceding year in the models did not change the findings. Furthermore, plant biomass did not significantly influence the FDis of gastropods and snails (data not shown).
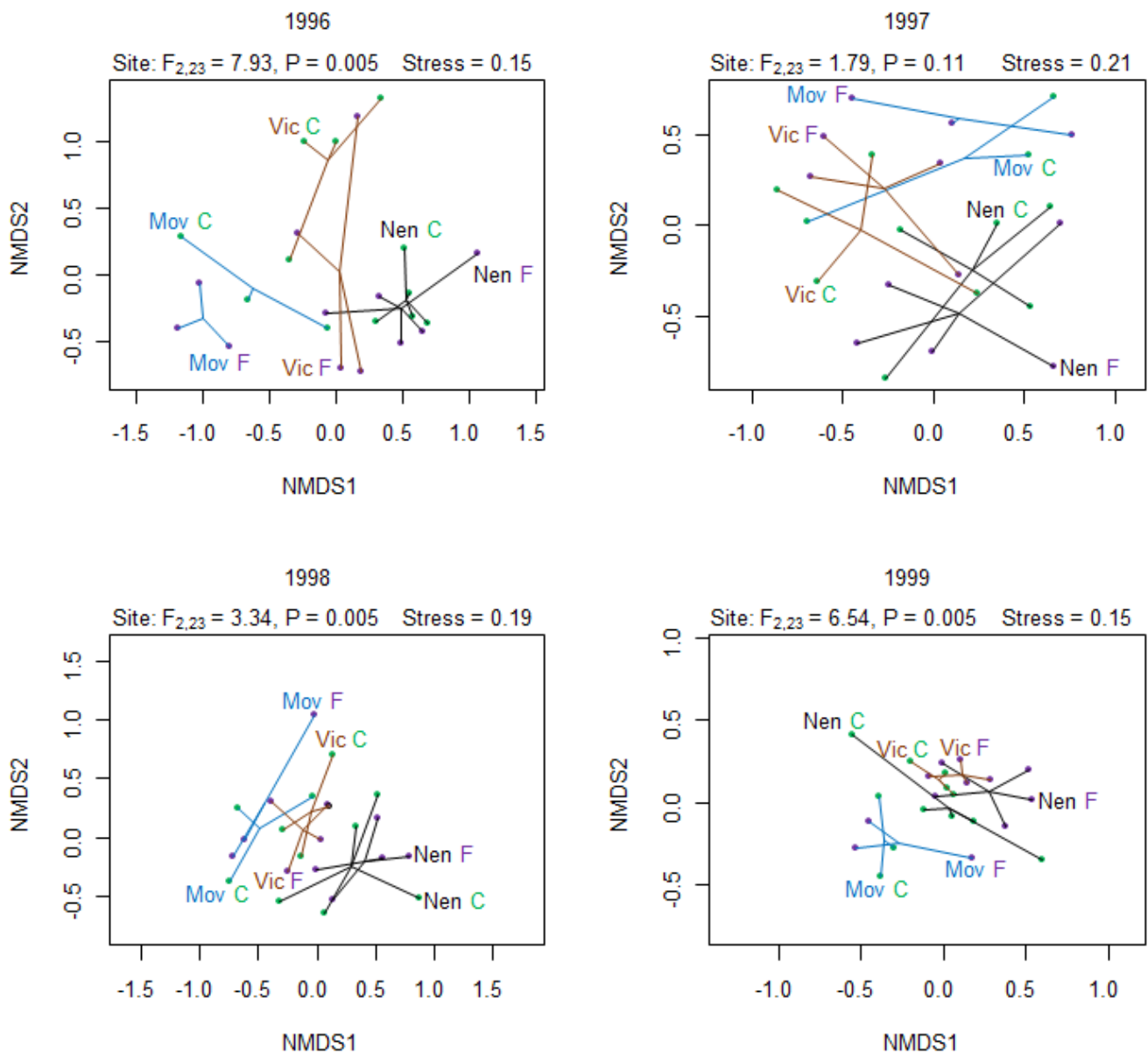
Figure 2. nMDS plots for species composition of all gastropods in fragments and control plots for each year. Sites are differentiated by the colour of the ordispider connecting the site dots (Movelier—blue; Nenzlingen—black; Vicques—brown). Violet dots indicate fragments, while green dots indicate control plots. PERMANOVA statistics for site effects are shown on top of the panels. No significant fragmentation effect was found in any year.

Table 3. Effects of experimental fragmentation on the functional dispersion (FDis) of all gastropods (snails and slugs combined) or of snails only, in the years 1996–1999. Significant *p*-values are displayed in bold.

	1996			1997 [1]			1998 [1]			1999		
(a) All gastropods	**df**	**F**	*p*	**df**	**F**	*p*	**df**	**F**	*p*	**df**	**F**	*p*
Fragmentation treatment	1,11	0.08	0.78	1,11	0.09	0.77	1,11	0.49	0.50	1,11	1.64	0.22
(b) Snails												
Fragmentation treatment	1,11	0.01	0.94	1,10	0.23	0.64	1,10	0.56	0.47	1,11	5.88	**0.034**

[1] One block each was omitted in 1997 and 1998 for analyses of snail FDis because they contained no snails in one of the plots.

3.5. Morphological and Life-History Traits

Body size, expressed as mean shell size of snail assemblages (weighted by the abundances of the various species), was not influenced by the experimental grassland fragmentation (Table S17). When the plant biomass of the preceding year is included in the models, plant biomass itself influenced mean shell size in 1998 and 1999 (it decreased with increasing biomass; Figure S2) and was only marginally non-significant in 1997 (Table S18). However, including plant biomass of the preceding year did not change the absence of a fragmentation effect on mean shell size (Table S18).

Fragments had a higher proportion of gastropod individuals belonging to species with an age at sexual maturity ≤1 year than large control plots in 1999 (Table S19). A similar effect was found for the proportion of snail individuals with age at sexual maturity ≤1 year in 1999 (Table S19). In the other years of the study, no significant effect was found (Table S19). Fragments also harboured a higher proportion of gastropod individuals with long lifespans (>2 years) than the corresponding control plots in 1999 (Table S20). This effect was even more pronounced for the proportion of snail individuals with a long lifespan in 1999 (Table S20). Thus, on average, gastropods in fragments matured earlier but lived longer than those in control plots in 1999.

3.6. Habitat Preferences

Experimental habitat fragmentation changed the proportion of generalist to open-land individuals (combined species with either of these habitat preference categories). Fragments contained a higher proportion of generalist individuals in 1998 (marginally significant for gastropods) and 1999 (highly significant for both gastropods and snails; Table S21). Furthermore, experimental habitat fragmentation affected the proportion of individuals with different humidity preferences. Fragments contained a higher proportion of individuals showing a preference for moist conditions than control plots in 1996 (both gastropods and snails) and in 1999 (only gastropods; Table S22).

4. Discussion

Our study showed subtle effects of grassland fragmentation on gastropod functional dispersion and on the relative proportions of individuals with certain traits or habitat preferences. Some of the effects increased in the course of the experiment, suggesting a time lag in the species' responses. Furthermore, the observed fragmentation effects varied over time. Slight fragmentation effects may not always be apparent because of varying environmental conditions (temperature, precipitation and plant biomass) between years and among sites (soil, historical development and type of management) [17]. In our experimental grasslands, plant biomass, gastropod individual density and species composition varied among the three sites. This may, in some years, have masked fragmentation effects, even though our models for separate years were corrected for site effects (by including site as random factor) and using a paired design with fragments and corresponding control plots in the same blocks. Additionally, precipitation varied strongly over the years. While 1997 was relatively dry, the final year of our study (1999) had the highest annual precipitation recorded for the years 1988–2021 at the nearby weather station in Laufen (almost 40% above the mean for these years; data from MeteoSwiss [45]). This may explain, at least in part, the high gastropod density recorded for that year.

A variety of plants and animals respond rapidly to changes in habitat quality and connectivity [41,55,56]. In many cases, however, there is a time lag in the response to the altered habitat [24]. The magnitude of this time lag depends on life-history traits, habitat specialism and the dispersal ability of the species involved [23,25]. The vast majority of the gastropod species inhabiting the studied grasslands have short generation durations [33,50] and limited dispersal ability [33], and 40% of them are generalists. This indicates that there was, for most species, a new generation each year in the experimental plots. Therefore, we expected short time lags in these species (see Löffler et al. [34]). Moreover, we started our gastropod surveys in the fourth year of the fragmentation experiment, thus allowing for

quick responses by the gastropod assemblages. Nevertheless, fragmentation effects on the relative density and species richness of snails (trends only), FDis of snails, proportion of individuals with early age at sexual maturity, proportion of species with long lifespans, and of proportion of habitat generalists were all most pronounced in the final year of our study (seventh year of the experimental fragmentation). This suggests that time-lags, even for such short-lived organisms, can be longer than expected. This finding strengthens the claim for long-term field experiments to assess the delayed effects of habitat fragmentation.

Habitats become subdivided at multiple spatial scales. Fragmentation ranges from small breaks in an otherwise-homogenous habitat to widely distributed small and large fragments in a hostile matrix [4]. Consequently, fragmentation experiments have been conducted at different spatial scales depending on the habitat requirements and activity ranges of various examined taxonomic groups and species (for a review see [20]). Fragmentation experiments focusing on openland invertebrates or small vertebrates have been primarily conducted at relatively small spatial scales [20,22,56,57]. In our field experiment, we used a relatively small scale with a fragment size comparable to those of grassland patches frequently found in gardens. This fragment size was sufficient to allow the existence of populations of several gastropod species (as shown by a mark–release–recapture approach [48]). The width of the matrix (5 m of short-turfed grassland) was chosen to represent the width of a local road, as they are frequent in the region [21]. It has been shown that real roads act as barrier for certain snail species [27,28]. The matrix in our experiment represents a relatively mild barrier not only for gastropods, but also for other invertebrate groups, when compared to paved roads and other sealed surfaces. Indeed, during summer, the hot and dry conditions of the matrix functioned as a barrier to gastropods, as well as a partial barrier for other taxonomic groups (butterflies [21] and bumblebees [58]). However, during winter, some specialized gastropod species (*Candidula unifasciata* and *Helicella itala*), which can be active in this season, were able to cross the matrix and recolonise fragments. Similarly, species with very large shells (*Helix pomatia*) were able to cross the matrix during longer periods of rain. It is important to note that even a partial (or a temporal) barrier that decreases dispersal impacts the population dynamics and genetics of the remnant populations in fragments [4,6].

In our study, we only considered living gastropods. The results were, thus, not confounded by a legacy of species present in earlier years that have since dwindled in fragments, but whose empty shells were still abundant. Indeed, given the short generation times of many species, individuals recorded in a particular year hatched from eggs in the preceding year and were, thus, mainly influenced by the conditions prevailing in the preceding year. It follows that almost all individuals recorded in our survey did not reflect the pre-fragmentation conditions, as would be the case for long-lived organisms.

Our study was part of a long-term fragmentation experiment, in which other taxonomical groups were also considered. This allows a comparison of fragmentation responses of various taxa within the same system. Short-term responses (in the fourth year of the experiment) in individual density to grassland fragmentation were shown for butterflies overall, as well as for 29% of 65 common species (ant, butterfly, gastropod and plant species [21]). Aphid individual density was higher in fragments than in control plots in the three years examined (the fifth to seventh year of the experiment [59]). Furthermore, after seven years, individual density differed between fragments and control plots in spiders, woodlice and the orthopteran species *Gryllus campestris* [22]. The direction of the response generally varied among species and taxonomic groups. For example, while the individual density of spiders was reduced in fragments in the seventh year of the experiment, it was increased in woodlice and *G. campestris* [22]. A time lag in response was found for overall ant nest density [60]. However, the individual density of ants (assessed using pitfall traps) did not differ between fragments and control plots, even in the seventh year [22]. In our study, we observed no fragmentation effect on species composition in gastropods. Similarly, no changes in species composition between fragments and control plots were found in ants or rove beetles in this fragmentation experiment [22]. However, significant alterations

in species composition were recorded after seven years of experimental grassland fragmentation in ground beetles, spiders and woodlice [22]. The combined results of these studies confirm that different taxa respond differently to the same type and spatial-scale of habitat fragmentation.

The experimental fragmentation altered snail FDis in the final year of our study. In contrast, the FDis of all gastropods was not affected by the fragmentation. There was, however, a time effect with the FDis of gastropods, which was higher in the fourth year of the study than in the other years. The findings for gastropods were partly influenced by the increasing numerical dominance of a single slug species over the course of our study (*Deroceras reticulatum*, a species known for high tolerance towards various types of disturbance [47]). This species occurred in almost all plots and accounted for 32.2% of all gastropod individuals in large plots in 1996, and for 61.6% by 1999. To our knowledge, FDis has rarely been examined in fragmentation studies. However, the frequently reported changes in species composition in fragments (e.g., ground beetles, spiders, woodlice [22] and wild bees [61]), in combination with the relationships between species' traits and fragmentation-affected environmental factors, suggest that FDis will often be affected.

In most animal groups, body size is related to dispersal ability, growth rate, home range size and maximum population density [62–64]. Large body size is expected to increase the probability of a species being present in a fragment, through an increased recolonisation rate. On the other hand, species with large body size may be at a disadvantage in maintaining sustainable populations in small fragments. Thus, it is not surprising that the relationship between body size and the species' vulnerability to habitat fragmentation is not straightforward [41]. Indeed, different studies reported contrasting results (no effect in beetles [65]; in grasshoppers, there were some species with larger body sizes in larger patches within landscapes with higher proportions of suitable habitat [37]; body size within local populations of some solitary wild bee species increased with fragmentation in flowering fields in an agricultural landscape [66]; there was a shift towards larger bee species in fragmented calcareous grassland [61]; and in woodlice, there were larger body sizes in disturbed and fragmented habitat than in undisturbed areas [38]). In our study, we did not find an effect of fragmentation on the mean shell size of snail assemblages in any year. However, mean shell size was related to plant biomass in some years, highlighting a possible indirect way in which grassland fragmentation can affect mean gastropod body size. In our field experiment, fragmentation changed plant biomass, vegetation structure and plant-species composition [35], each of which may affect habitat quality for some gastropod species in a different way.

Our results, which determined that the mean shell size of a snail assemblage in a plot was not affected by the experimental fragmentation, contrast the earlier findings of a mark–release–recapture study considering six snail species (ranging in size from 1.4 to 16 mm) by Stoll et al. [48]. Large snails are able to withstand the dry and hot conditions in a short-turfed matrix better than small snails [67,68]. Indeed, recolonization events were less likely in small fragments than in small control plots for the group of four small-sized snail species, while this effect was no longer significant if the two larger snail species were included in the analysis [48].

In the final year of our study, we recorded a higher proportion of gastropod individuals belonging to species attaining sexual maturity early, and which have longer lifespans, in fragments than in control plots. We expected the first response, as stressful environmental conditions have often been linked to species which attain sexual maturity early [40]. Given the short generation length of most of the considered gastropod species (≤ 1 year) in the grasslands, at least four generations had already passed for these species by the time we started our gastropod survey. All the gastropod species recorded are hermaphrodites, and most are able to self-fertilize [33]. These reproductive characteristics allow a single individual to reproduce immediately upon reaching sexual maturity.

A species' response to fragmentation may depend on a combination of different traits and habitat preferences [65]. Theory predicts that generalists should be less influenced

by habitat fragmentation than specialists [64,69–71]. In our study, the proportion of gastropod individuals belonging to habitat-generalist species was increased in fragments in the final two years of our study. Abiotic conditions in fragments differ from those of continuous grassland due to edge effects [21,71]. In the fragmentation experiment used by us, Zschokke et al. [21] recorded increased temperature in the edge zones of fragments, and Dolt et al. [35] reported changes in vegetation structure and plant biomass in the edge zones of fragments, which was assumed to affect humidity. This may explain why the proportion of individuals of species showing a preference for moist conditions increased in fragments in our study.

5. Conclusions

Most of the short-lived invertebrate species show huge yearly fluctuations in abundance. Therefore, snapshot studies considering only one season may lead to wrong conclusions on fragmentation-related effects. It follows that multi-year field studies are required to disentangle fragmentation effects from the background variation in the abundance of given species. Natural grassland fragments vary in size, shape (and, thus, in the amount of edge), age, and degree of isolation [5,6]. This complicates any analysis, and makes it difficult to distinguish between different factors that may cause changes in abundance and the local extinction of plant and animal species. The various sources of uncontrolled variation can be circumvented by applying an experimental approach, with standardized fragments and appropriate control plots at different field sites [20]. Thus, experiments allow for the demonstration of subtle effects, which would not be detected in natural fragments. Armed with these findings, follow-up studies can then focus on demonstrating observed fragmentation effects in real situations, such as populations on either side of a road. It should be mentioned, however, that experimental field studies are only feasible at small spatial scales, and not at the landscape scale. Interestingly, the fragmentation effects observed in our study were related to FDis and to the relative proportions of individuals exhibiting certain traits and habitat preferences, rather than to the frequently studied metrics of species richness and individual density. However, these shifts in trait distributions may further affect the functioning of ecosystems in fragmented grasslands.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d14060474/s1, Figure S1: Non-metric multidimensional scaling plots for species composition of snails per year; Figure S2: Relationships between snail-shell size and plant biomass of the preceding year; Table S1: Abundances of all species in each experimental plot in 1996; Table S2: Abundances of all species in each experimental plot in 1997; Table S3: Abundances of all species in each experimental plot in 1998; Table S4: Abundances of all species in each experimental plot in 1999; Table S5: Traits and habitat preferences for each species; Table S6: Mean plant biomass for experimental plots in each of three years; Table S7: Summary of ANOVAS with repeated measures for gastropod and snail density; Table S8: Pairwise comparisons for density of gastropods and snails between years; Table S9: Summary of models testing the effects of experimental fragmentation on plant biomass in the years 1996–1998; Table S10; Summary of models examining effects of experimental fragmentation and plant biomass of the preceding year on the density of gastropods and snails in the years 1997–1999; Table S11: Summary of ANOVA with repeated measures for species richness of gastropods and snails; Table S12: Pairwise comparisons for species richness of gastropods and snails in fragments and control plots between years; Table S13: Summary of models testing the effects of experimental fragmentation on species richness of gastropod and snail assemblages in experimental plots in the years 1996–1999; Table S14: Summary of models testing the effects of experimental fragmentation and plant biomass of the preceding year on species richness of gastropods and snails in the years 1997–1999; Table S15: Summary of ANOVAs with repeated measures for FDis of gastropods and snails; Table S16: Pairwise comparisons for FDis of gastropods in experimental plots between years; Table S17: Summary of models testing the effects of experimental fragmentation on the mean shell size of snails in the years 1996–1999; Table S18: Summary of models testing the effects of experimental fragmentation and plant biomass of the preceding year on the mean shell size of snails in the years 1997–1999; Table S19: Difference in proportion of age-at-sexual-maturity classes (≤1 year, >1 year)

of gastropods and snails, respectively, in fragments and control plots in the years 1996–1999 with Fisher's exact tests; Table S20: Differences in proportions of longevity classes of gastropods and snails, respectively, in fragments and control plots in the years 1996–1999 with Fisher's exact tests; Table S21: Differences in proportions of individuals with certain habitat preferences (habitat generalists vs. openland species) of gastropods and snails, respectively, in fragments and control plots in the years 1996–1999 with Fisher's exact tests; Table S22: Differences in proportions of individuals with certain humidity preferences (wet, moist and dry) of gastropods and snails, respectively, in fragments and control plots in the years 1996–1999 with Fisher's exact tests.

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