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Habitat fragmentation experiments on arthropods: what to do next?

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Habitat fragmentation has the potential to influence ecological and evolutionary dynamics in various ways. Fragmentation experiments explore these multiple influences and the underlying mechanisms. We review experiments used in arthropods and highlight gaps in biological focus, methodology and questions addressed. While the consequences on community structure were often reported, fewer studies focused on ecosystem functions and evolutionary processes, with striking gaps on genetic and eco-evolutionary dynamics. Regarding fragmentation components, matrix quality was often overlooked while inter-patch (and source-patch) distance was the most studied component. The identified gaps outlined our need to study fragmentation at different time-scales, and on teasing apart the respective roles of each fragmentation component on each eco-evolutionary process.

Keywords: habitat fragmentation, arthropod, insect, review, experiment, eco-evolutionary dynamics, species traits

INTRODUCTION

Habitat loss and fragmentation profoundly alter biodiversity [1], although some debated data recently suggested potential benefits of fragmentation *per se* [2–4]. Habitat fragmentation involves the transformation of large expanses of habitat into a number of smaller patches of smaller total area, isolated from each other by a matrix of altered habitat [5]. It involves the conjunction of four components: (a) reduction in habitat amount, (b) increase in the number of habitat patches, (c) decrease in patch size, and (d) increase in patch isolation [6]. Consequently, the edge-to-core habitat ratio also increases with fragmentation [7]. The relative importance of these components on biodiversity may vary between landscapes, making the investigation of fragmentation impacts complex. This investigation is further hampered by the confounding effects on biodiversity between fragmentation *per se* (i.e., the breaking apart of habitat, controlling for changes in habitat amount, [6]) and reduction in habitat amount. As habitat fragmentation is inherently linked to habitat loss in most landscapes, there is a correlational structure between the effect on biodiversity attributable to habitat loss and to fragmentation *per se* [8]. Further, fragmentation may have confounding, synergetic and/or antagonist effects with other global change aspects such as urbanisation, climate change or biological invasions [9–11]. Fragmentation effects might also be nonlinear but increase exponentially after a threshold of habitat loss (e.g. [12,13] but see [14]), which might be especially relevant given the dire predictions for future habitat degradation [15]. Such complexity pleads for using experimental approaches to better estimate the relative consequences of different fragmentation components [16], the interactive effects with other abiotic and biotic drivers and the effects at different spatio-temporal scales, potential sources of discordance in results [3]. While “natural experiments” (sensu Diamond 1986 [16], i.e. field observations) escape spatio-temporal scale issues and benefit from higher realism and applicability, laboratory and field manipulative experiments (Hurlbert 1984 [17]) allow to disentangle between the effects of correlated components

fragmentation, test for interactive effects of other ecological factors, and tackle mechanisms behind biodiversity changes. Here, we aim at providing an overview of the current experimental approaches testing for habitat fragmentation consequences in arthropods.

Arthropods constitute a major part of biodiversity [18] and provide fundamental ecosystem services [19]. As small ectotherms, arthropods might be especially sensitive to the accumulation of physical, biotic and climatic dispersal barriers created by fragmentation [20]. Further, many arthropods depend on multiple habitats (aquatic, terrestrial or aerial) during their ontogeny, imposing distinct constraints on movement. Unfortunately, the number of fragmentation studies on arthropods is not proportional to their biological importance and sensitivity to fragmentation [2,21].

We created a data base of existing experiments on habitat fragmentation on arthropods using a systematic review of the literature. From this database, we aimed to provide a full picture of how fragmentation has been manipulated in arthropod experiment by classifying the taxa, the biological level, the fragmentation components manipulated and the response variables. We also aimed to identify gaps in the questions addressed and potential shortcomings in experimental approaches. We searched Web of Sciences with `experiment* AND fragment* OR main fragmentation components OR metasystem type` (see Supplement for exact search), yielding 5865 articles, of which 212 were finally included (Fig S1). Criteria for inclusion comprised (a) study involves arthropods, (b) is a manipulative experiment (sensu [17,22]) performed through landscape manipulation in the field or in the laboratory, and (c) focuses on one or more of the above defined fragmentation components, irrespectively of their distinction of fragmentation *per se*. Natural experiments (sensu [16]) without landscape manipulation *per se* (e.g. translocation between landscapes) were therefore excluded. Our aim was to provide a full picture of how fragmentation has been manipulated in arthropod experiments. The identified gaps were used to propose guidelines to improve our understanding of fragmentation impacts.

BIOLOGICAL FOCUS OF STUDIES

A third of the studies focused on large arthropod communities, and a quarter on a single species (Fig 1A). The most investigated insect orders were Coleoptera, Hymenoptera, Lepidoptera and Hemiptera, and the most investigated non-insect classes were Arachnida and Malacostraca (Fig S2A). Formicidae, Apidae, Aphididae and Delphacidae were well represented families (Fig S2B); *Prokelisia crocea* (planthopper), *Anagrus columbi* (fairyfly) and *Junonia coenia* (butterfly) were the most studied species. Surprisingly, very few studies used model species like *Drosophila*, *Culex* or *Bombyx* (but see [23,24]), at the exception of bees and, to a lesser extent, *Daphnia*.

Aquatic systems were particularly neglected as well as their interface with terrestrial environments (Fig 1, but see [25]). Insects with complex lifecycles (e.g. dragonflies) might undergo different eco-evolutionary pressures induced by fragmentation during ontogeny, potentially affecting ecological dynamics at a regional scale even when fragmentation occurs at very local scales.

More than half of the studies focused on the community level, and drew general inferences mostly on fragmentation effects on species richness and abundance. While understanding how fragmentation modifies interaction strengths is crucial to assess its impacts on community dynamics, very few studies tackled species interactions, in particular competitive strengths (Fig S3B). Within species, roughly equal number of studies focused on population abundance and dispersal or movement. Fewer studied focused on other phenotypic traits, and only one study on genetics (Fig S3C). This points out a lack of evolutionary consideration, with 1% of studies explicitly testing evolutionary processes.

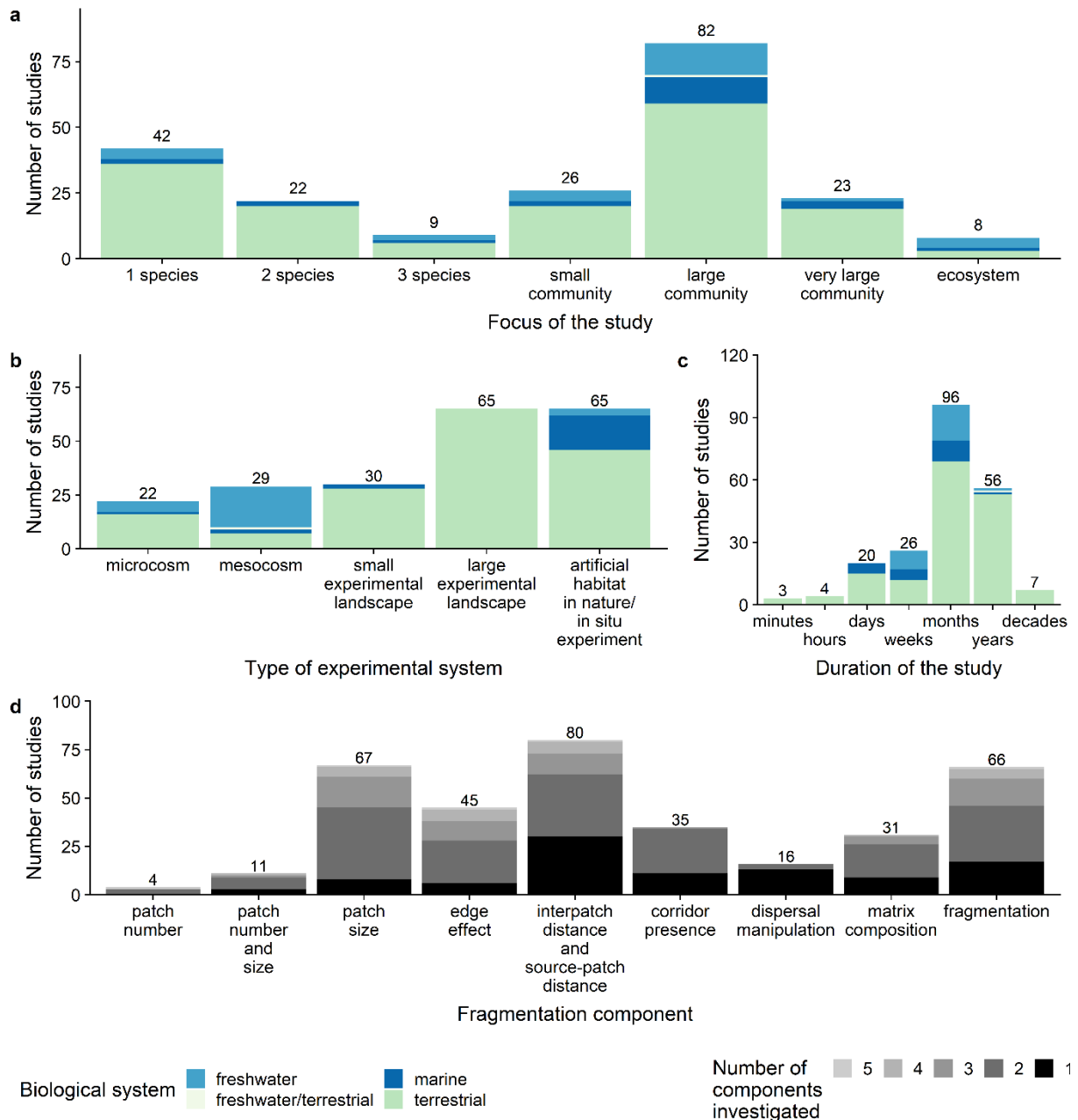


Figure 1: Number of studies by biological focus, type and duration of experiment and fragmentation components.

(a) Biological focus of the study. Small communities are <10 species, large communities <100 species and very large communities >100 species, the ecosystem category is for studies focusing on ecosystem functions. (b) Type of experimental setting. Microcosms (<1 m²) are divided into indoor microcosms (16 studies), outdoor microcosms (1 study), and undefined (5 studies). Mesocosms (>1m²) are divided into indoor mesocosms (3 studies) and outdoor mesocosms (26 studies). Small experimental landscapes are <1ha, and large >1ha (see Supplement for discussion of area). The last category involves studies manipulating landscape features in natura. (c) Duration of the study. (d) Type of fragmentation components investigated. Notice that the total number of studies for this plot is more than 212 as several studies focus on more than one fragmentation component. Also notice that “fragmentation” defines studies where all components vary together, for instance “continuous vs fragmented”.

While arthropods are crucial for many ecosystem functions (e.g., nutrient cycling [19]) themselves affected by fragmentation [26], only 5% tackled ecosystem functions or related relevant traits like biomass and decomposition rate (Fig 1A, Fig S3C).

EXPERIMENTAL SETTINGS AND FRAGMENTATION COMPONENTS STUDIED

Forty-four percent of the studies made use of small or large experimental landscapes, 30% manipulated landscape features *in natura* and only 24% used micro- or mesocosms (Fig 1B). Study duration varied from minutes to decades, but was predominantly months (Fig 1C, see supplement for discussion on generation times). Having decade-long studies such as [27–29] is an asset as time lags are crucial in understanding the effects of fragmentation, with potentials for extinction debts arising [30].

Half of the studies were designed to isolate the effect of one component (e.g. patch number, inter-patch distance, matrix composition), the others investigated 2 or more components (Fig 1D) with more than half manipulating all fragmentation components at the same time. The latter mainly contrasted two fragmentation levels (continuous/fragmented) while fewer used 3 levels (continuous/slightly fragmented/highly fragmented) or more (Fig S4A), despite the fact that fragmentation processes are non-linear [12,13]. Patch size and edge effect were frequently studied, in comparison to the number of patches. Connectivity was studied through the manipulation of inter-patch distance, corridor presence or dispersal manipulation, but rarely through matrix composition modification (Fig 1D).

Interactions between fragmentation and other aspects of global changes can represent deadly cocktails for biodiversity [9]. However only 6% of experiments also manipulated other aspects of global change (temperature, pollution, invasive species). More generally, only 33% and 13% of the studies manipulated or quantified the biotic quality (mainly vegetation composition) and the abiotic quality (e.g. salinity, nutrients) of patches respectively.

As previously outlined [31], we observed a trade-off between ecological realism and the number of experimental replicates within studies (Fig S4B). This trade-off is further compounded when multiple studies use the same experimental landscape, thus decreasing the ecological replication among ecosystems. Indeed, half of the studies on large experimental landscapes hinged on four projects only (Savannah River Site, Miami research center, Wog Wog or BDFFP project). On the one hand, the detailed consequences of fragmentation on well-known experimental systems provide unique comparative power that deserves special attention. On the other hand, the low ecological replication might lead to over-generalising results potentially idiosyncratic and dependent on specific features of the studied systems. Particularly, most of the studies focus on forests or grasslands [31] and are located in temperate zones [21]. Results that apply to these ecosystems might not be extendible to other regions and/or ecological biomes. We urge to increase the ecological replication of experimental settings, especially adding new large/small experimental systems in diverse regions and ecological biomes including at the terrestrial/aquatic interface.

WHAT TO DO NEXT?

Despite a wide breadth of experimental studies either directly- or indirectly-focused (e.g. meta-system's literature) on habitat fragmentation, we confirmed previous identified gaps, and highlighted unexpected ones in the biological focus, questions, fragmentation components studied (Fig 2, Table S1A-C) and methodology used (Table S1D). We hereafter suggest improvements of experimental studies. As our goal was not to compare experimental and non-experimental studies, identified gaps may also (and often do) apply to non-experimental studies.

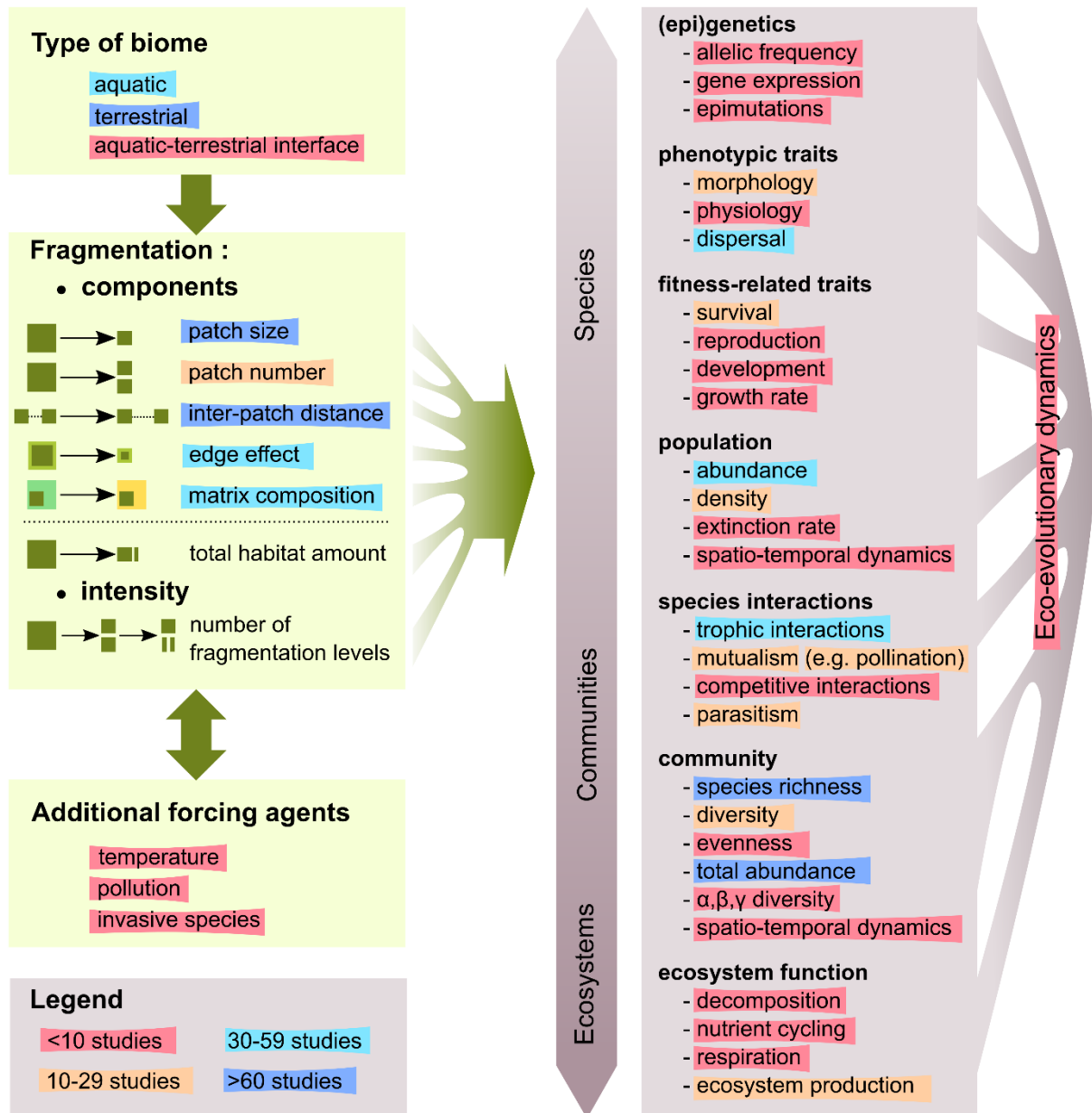


Figure 2: Summary of the potential impacts of fragmentation components on different levels of biodiversity, and gaps in our understanding of these impacts. Concepts are underlined in different colours depending on the number of studies in which they are investigated. Concepts underlined in red represent strong gaps in our understanding (see Table S1 for a more detailed analysis of the gaps), with below 10 studies tackling them. Concepts in orange were tackled by 10-29 studies, in light blue by 30-59 studies and in dark blue by >60 studies. Notice that for each biological level, we underline only a few aspects (e.g. under phenotypic traits, we detail morphology but not behaviour).

Our main takeaway is that a large portion of experiments usefully describe changes in community structure, but rarely examine the underlying changes in species interaction and the subsequent changes in community dynamics. Such gaps on species interactions were highlighted 20 years ago [31], with some improvements in the recent years for arthropods (Fig S5). We also lack studies on ecosystem functions such as decomposition rate, which is key to nutrient cycling. Future fragmentation experiments on arthropods should therefore shift from community descriptive

investigation to the study of species interactions and consequences on ecosystem functions. Dedicated fragmentation platforms should help to achieve these goals [32,33]. Although a significant number of studies focused on the species level, the evolutionary consequences of fragmentation were largely ignored, with the exception of dispersal-related studies, which were pointed out as a gap 20 years ago [31] that have been partly filled since (Fig S5). Therefore, the respective roles of adaptation, drift, plasticity or mutation in the response to fragmentation are little known in arthropods. This knowledge is however crucial to correctly interpret patterns and predict biodiversity changes. This limited interest for the evolutionary consequences of fragmentation explains why theoretical predictions about the role of fragmentation in eco-evolutionary feedbacks remain untested [34]. Future studies should thrive to understand how species traits, but also genomes, evolve with fragmentation in complex biological settings where interacting species can jointly co-evolve. The development of omics and/or use of arthropod models such as *Drosophila* or *Daphnia* should help to achieve such mechanistic goals. Coupling these experimental studies with both theoretical models and validation in the field should help better understanding how eco-evolutionary processes affect arthropod biodiversity.

Regarding fragmentation components, matrix composition remains poorly studied since Debinski and Holt's review [31]. While matrix is at the core of fragmented landscapes [26,35], its resistance, a fundamental parameter to assess functional connectivity [36], is understudied, and has been called for. We also call for an increase in the type of ecological biomes studied with large replication within landscapes, and for more numerous levels of habitat fragmentation with continuous landscapes as controls. Finally, we urge for the integration of other components of global changes in fragmentation experiments. Climate change, pollution and the spread of invasive species can often co-occur with habitat fragmentation. Experimenters should aim at assessing interactions and eco-evolutionary consequences of these multiple global change drivers.

To conclude, we hopefully provided an objective synthesis of what is known, and what is unknown from fragmentation experiments in arthropods. To this end, we searched for all experiments, irrespective of their integration of only patch-scale or landscape-scale processes, and their control for habitat amount. While such information is obviously crucial to better capture the complexity of fragmentation (and is available from our database), we are convinced that among scientists' general interests, one crucial goal is to describe patterns and mechanistically explain them, avoiding judgement on potential beneficial and deleterious effects. It is hazardous to decide, for example, if an increase in species abundance or diversity is beneficial given that any change in ecological networks due to fragmentation can have detrimental consequences for ecosystem functioning as a whole. For instance, an increase in Orthoptera abundance with fragmentation [37] can negatively affect plant biomass [38], with potential cascading effects on belowground species and ecosystem function [39]. It might even occur that these fragmentation-induced changes feedback to habitat fragmentation itself through eco-evolutionary loops [34]. In the future, we hope that long-term experiments will bring elements to feed such questioning and to inform on long-term stability and recovery of anthropized systems.

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Supplementary Material for

Habitat fragmentation experiments on arthropods: what to do next?

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Current Opinion in Insect Science 2019, 35

Includes:

Supplementary Methods

Figure S1: Flow chart detailing the process of study identification, selection and data extraction

Figure S2: Number of studies focusing on each taxon (A: order, B: family)

Figure S3: Design of the fragmentation studies in terms of secondary measures and eco-evolutionary processes investigated

Figure S4: Number of fragmentation levels, and mean number of landscape replicates per studies

Figure S5 Cumulative number of studies over the years investigating several topics of importance

Table S1: Identified gaps and suggestions for closing them

References cited in the supplementary material only

Complete list of studies selected for the review

Supplementary Methods

We created a data base of existing experiments on habitat fragmentation on arthropods using a systematic review of the literature. From this database, we aimed to provide a full picture of how fragmentation has been manipulated in arthropod experiment by classifying the taxa, the biological level, the fragmentation components manipulated and the response variables, and to identify gaps in the questions addressed and potential shortcomings in experimental approaches. Note that our database was focused on experimental studies, and we did not provide a comparison with non-experimental studies because we did want to opt for point-scoring between the two valuable experimental and non-experimental approaches. We also did not examine whether fragmentation effects were beneficial or detrimental as it would require a proper meta-analysis and we consider that any change, increase or decrease of a biological metric (e.g. species abundance) can be detrimental at wider ecological scales (see discussion).

We conducted the literature search in two steps: a first step in which we used only the keywords fragmentation AND experiment* (see below), from which we got 2496 results that we then filtered through a two-step exclusion process to get to a set of 159 articles from which we extracted data for our quantitative overview, and a second step in which we used more keywords that we directly derived from the 166 article database, yielding 3369 more articles of which 53 were included. This two search steps procedure allows to avoid forgetting certain types of keywords by searching for keywords that were often present in our initial search and completion of the database. In total, this two-step procedure led to the building of a database of 212 articles. Figure S1 shows the process of study identification, selection and the data extracted from each relevant article.

We first searched Web of Knowledge for the keywords fragmentation AND experiment*, refining for Web of Science Categories biodiversity conservation OR biology OR ecology OR entomology OR environmental sciences OR evolutionary biology OR forestry OR marine freshwater biology OR microbiology OR plant sciences OR soil science OR zoology. The search, undergone in November 2018, revealed 2496 results. We did not include taxonomic information in the search terms to avoid excluding articles where the keywords and abstract did not include taxonomic information, or too specific taxonomic information that would be impossible to search for, but chose to exclude non-taxonomically relevant studies during the first filter. Notice that by focusing on experiment*, we certainly miss studies that were experimental by nature but did not state it explicitly. We used two-step procedure to reduce the 2496 articles to a list of 159 articles fitting our inclusion criteria, first examining the title and abstract, and second examining the full text of the remaining studies and extract information (see below). Examining the full text allowed to identify more keywords that we then used in a second step of search to complete our database. In this step, we focused on studies that would not have fragmentation as a topic but a shorter version of the word (e.g. fragmented), searching for TOPIC: (fragment* AND experiment* NOT fragmentation) Refined by: Web of Science Categories: (Ecology OR Environmental Sciences OR Entomology OR Evolutionary Biology OR Marine freshwater biology OR Plant Sciences or Zoology). Timespan: 1975-2018. We also searched for studies that did not have the fragmentation keyword in the topic but could have keywords linked to one of the fragmentation components that we identified in our first search and analysis of the database, and keywords linked to meta-systems, with the search TOPIC: ((patch number) OR (patch size) OR (edge effect) OR (patch distance) OR (patch isolation) OR (corridor) OR (matrix composition) OR (metapopulation*) OR (metacommunit*) OR (metaecosystem*) OR (meta-population*) OR (meta-communit*) OR (meta-ecosystem*)) AND (experiment*) NOT (fragmentation) Refined by: Web of Science Categories: (Ecology OR Evolutionary Biology. Timespan: 1975-2018. This second step of search yielded 3369 more articles, which were then filtered through our two-step exclusion process in the same way as the articles issued from the first step of search.

From the list of 2496 original articles, and from the list of 3369 articles from the second search, we examined each title and abstract to determine whether articles met the criteria for inclusion in our overview of the literature. Criteria for inclusion comprised (a) the taxonomic identity of the species or group of species studied, keeping only studies that involved arthropoda, (b) the fact that the study was a manipulative experiment (*sensu* [17]) by manipulating landscape features, and (c) the fact that the study focused on one or more of the four aspects of habitat fragmentation defined by [6], that is reduction in habitat amount, increase in the number of habitat patches, decrease in the size of habitat patches, and increase in the isolation of habitat patches. We included papers on habitat fragmentation *per se* (without habitat loss) and papers where the manipulation of fragmentation was linked to a loss of habitat, but not papers that manipulate only habitat loss (exclusion of papers manipulating only patch size). We excluded review papers, purely theoretical papers, and papers that did not fit our definition of experimental, that is a manipulative experiment *sensu* [17] instead of a mensurative experiment. For instance, we excluded capture-mark-recapture studies that did not explicitly manipulate fragmentation, but only captured individuals present in habitats with various levels of fragmentation, which corresponds more to a mensurative experiment. We also excluded studies that e.g. used pitfall traps to recover insects present in naturally fragmented habitat, if there was no manipulation of the habitat. However, we included all manipulative experiments irrespective of the strength or statistical significance of the results. At times, the title and abstract were too vague to positively assess these three criteria of inclusion, and the articles were kept for further detailed reading of the text; they could be thus excluded in a second filtering session. The first filtering session led to a selection of 345 studies from the original search and 199 studies from the second step of search that fitted the scope of this overview (Fig S1).

The remaining 345 original articles and 199 articles from the second search were then reviewed in full to determine whether they fitted our inclusion criteria, contained relevant data and whether the results were presented with sufficient clarity (Fig S1). This step led to the further exclusion of 186 articles from the first search and 146 articles from the second search. From the final set of 212 studies, we then extracted data relevant to several questions:

- 1) In which kind of ecological system was fragmentation studied (terrestrial, freshwater, marine)?
- 2) Which was the biological focus of the study: species level, two- or three-species level including e.g. pollination or predator-prey interactions, community level (small community, <10 species, large community, <100 species, very large community, >100 species), ecosystem level? Which taxa were considered? When studies focused on less than four species, we noted the three species studied. When studies focused on more species, we noted the main taxa studied (e.g. Aphidae and Coccinellidae, maximum three taxa at the lower level to avoid listing each and every taxon in very large communities).
- 3) Which type of experimental setting was used: artificial habitat in nature/natural landscape, small experimental landscape (<1ha) large experimental landscape (>1ha), indoor or outdoor mesocosms (>1m), indoor or outdoor microcosms (<1m)? Which kind of experiment was done: landscape manipulation, translocation, dispersal manipulation? Notice that the size of experimental landscapes was arbitrarily divided into small and large based on the 1ha threshold to simplify analyses, but the scale of habitat fragmentation might depend on the size of the organism studied and the question posed. For instance, 100 m² is a very large landscape for a mite, but quite small in terms of home range for a dragonfly. Further, studies on dispersal might need very big landscape sizes when focusing for example on dispersal distances, but might be more small-scaled when focusing for example on emigration decision [32,40]. Notice also that while moss systems are correctly considered as natural microcosms, we decided to classify them as artificial habitat in nature/natural

landscape in our study, at the rare exception of studies enclosing mosses in incubators (classified here as microcosms).

4) Which was the focus of the fragmentation study: e.g. patch number or size, inter-patch distance, patch-source distance, edge effect, corridor, matrix composition? Which other features non-directly related to the fragmentation were studied (e.g. biotic or abiotic patch quality)? As habitat amount is inherently linked with many components of the general fragmentation process (e.g. patch size, patch number), and we did not aim to separate habitat fragmentation *per se* from more general fragmentation, some components may covary with habitat loss.

5) What was the duration of the study: minutes (up to 59), hours (up to 23), days (up to 6), weeks (up to 3), months (up to 11), years (up to 9), decades? Because extremely few studies reported time in generations, we only report calendar time. However, studies within the same time scale might mean completely different things for long-lived, long generation time species such as cicadas and short-lived, short generation time species like acari.

6) What were the metrics studied: e.g. community structure, population abundance, survival, interspecific interactions, dispersal, phenotypic traits?

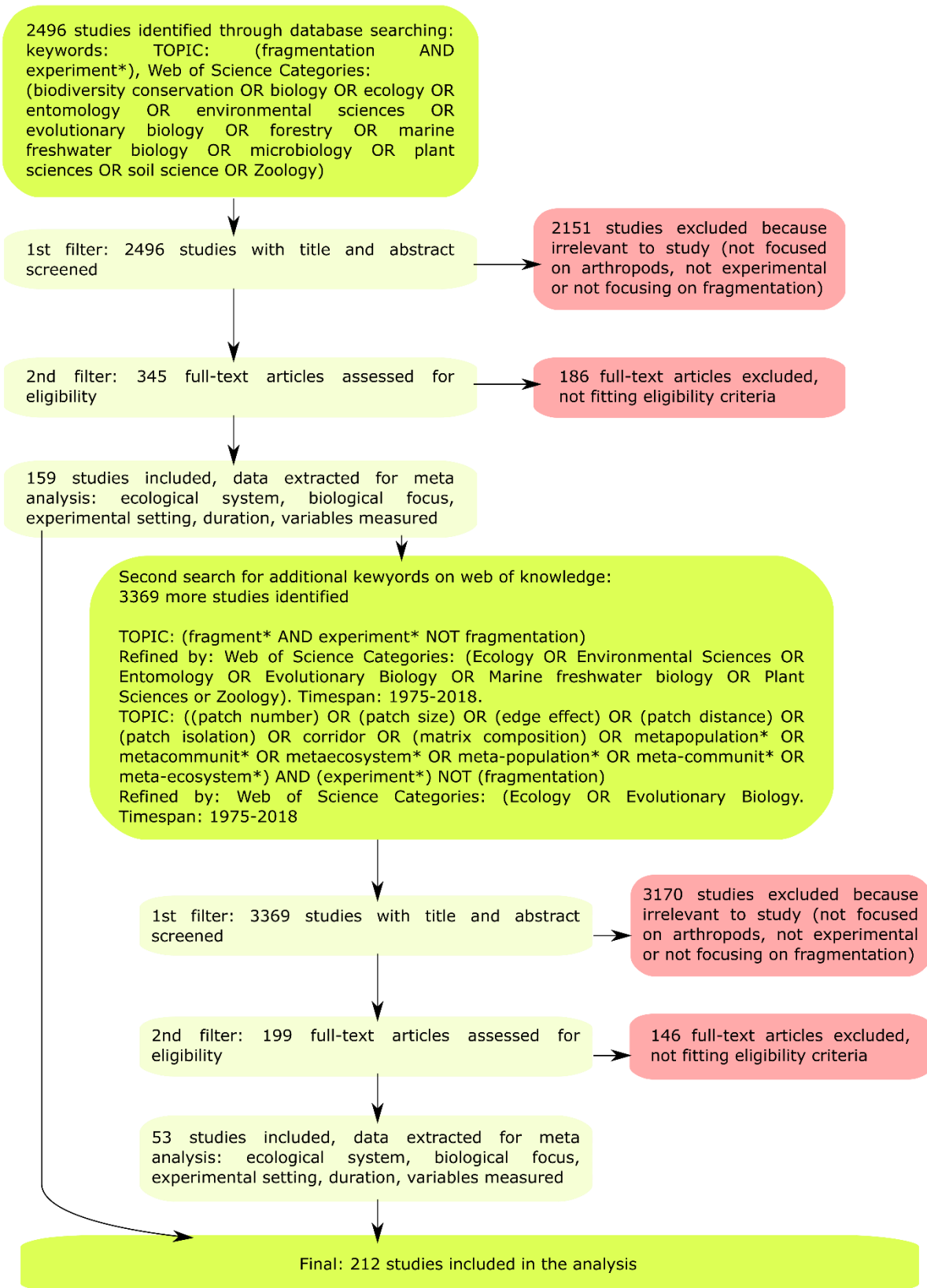


Figure S1: Flow chart detailing the process of study identification, selection and data extraction

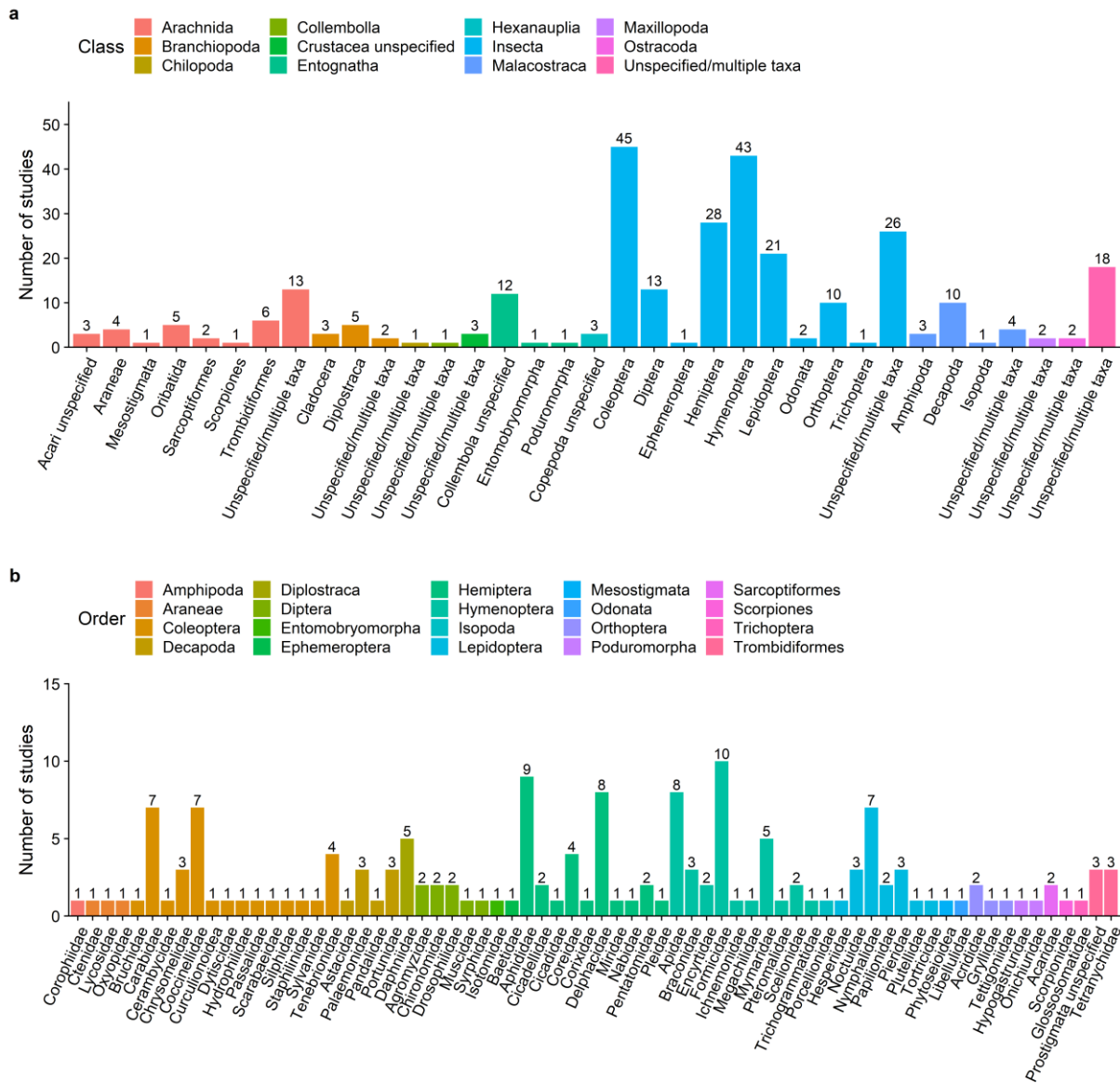


Figure S2: Number of studies focusing on each taxon (a: order, b: family)

Please note that studies that involved more than 3 taxa (resp. order or family) were not taken into account when counting the number of studies using a specific taxon, as it would be complicated to track each and every taxon used in studies on large communities. Also note that the sum of the number of studies investigating each taxon can be superior to the total number of studies as each study can investigate several taxa.

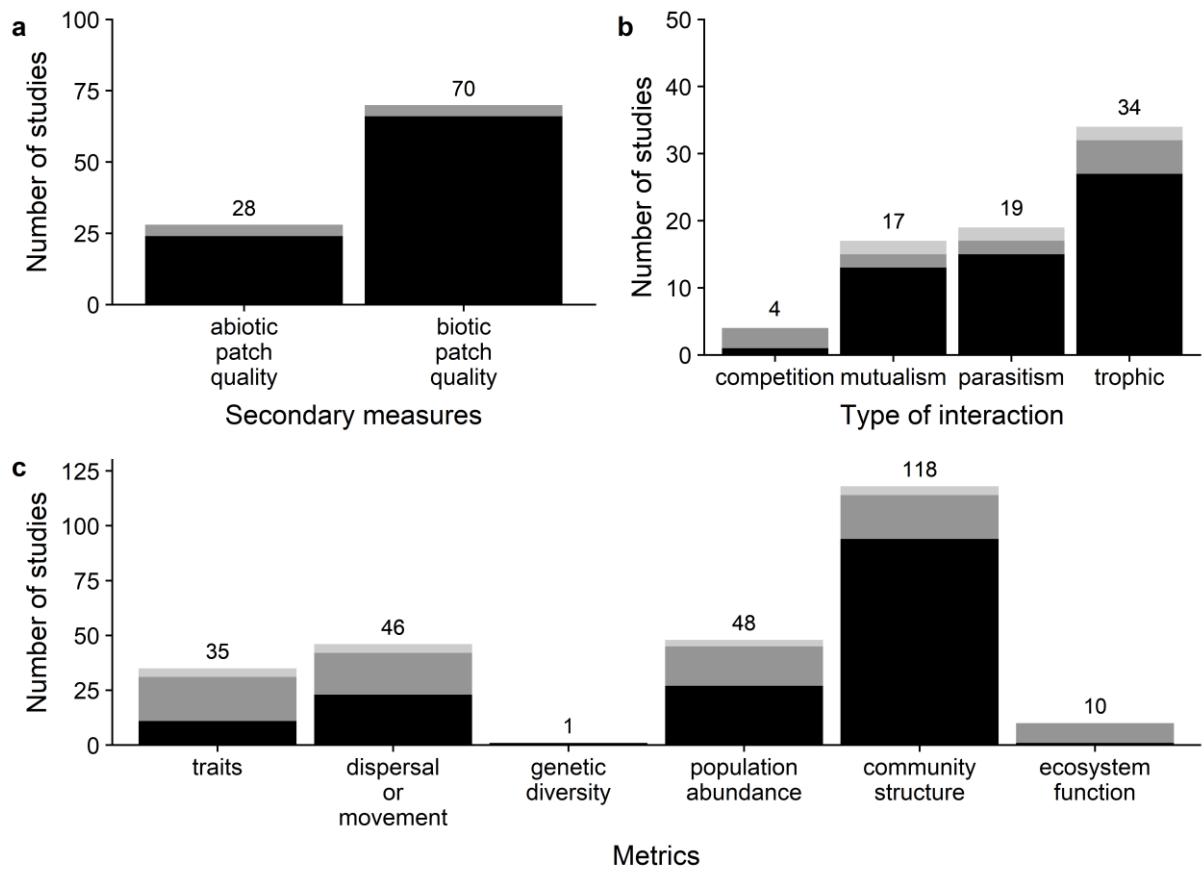


Figure S3: Design of the fragmentation studies in terms of secondary measures and eco-evolutionary processes investigated

Note that the total number of studies mapped is superior to the number of studies assessed, as one study can investigate several fragmentation processes and several metrics at once. Black bars: studies that tackled only one measure/feature/metric, grey bars: studies that tackled multiple measures/features/metrics at once (dark grey: 2 measures, light grey: 3 measures)

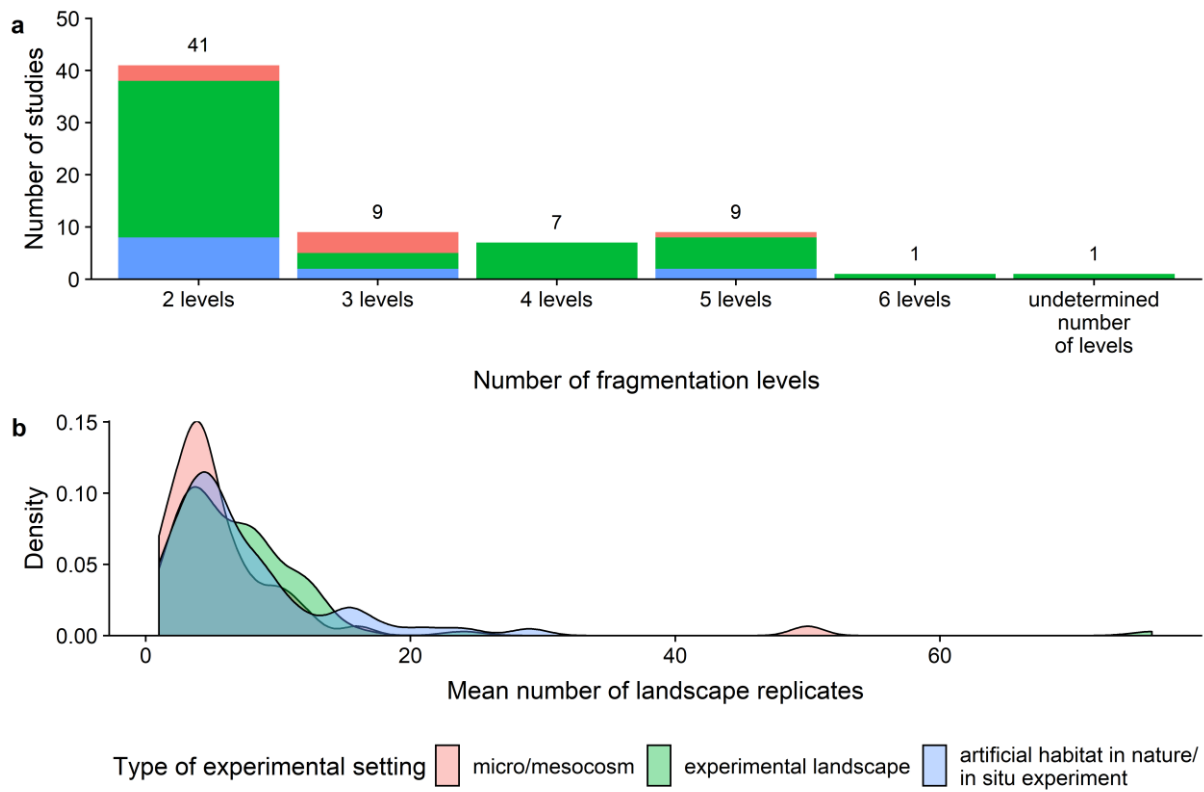


Figure S4: Number of fragmentation levels, and mean number of landscape replicates per studies

(a) In “continuous vs fragmented” designs, where all components of the fragmentation process vary at the same time, the number of levels of fragmentation used (e.g. continuous/low fragmentation/high fragmentation equals 3 levels). (b) Density plot of the number of landscape replicates per treatment in the studies, separated by type of experimental setting.

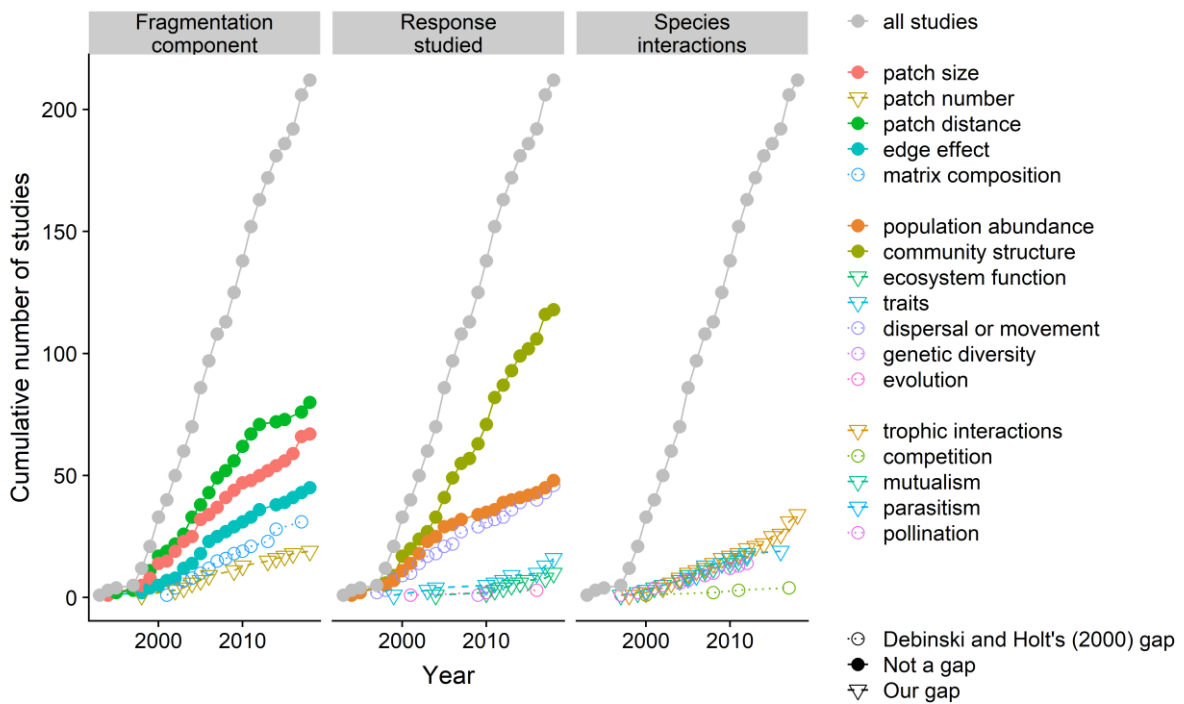


Figure S5 Cumulative number of studies over the years investigating several topics of importance

Dotted lines and empty circles represent the gaps highlighted by Debinski and Holt in 2000 [31], while dashed lines and empty triangles represent gaps highlighted in this review and full lines and filled circles represents topics that are not considered as gaps.

Table S1: Identified gaps and suggestions for closing them

(a) identified gaps on the biological focus of the study. (b) Identified gaps on the type of ecological and evolutionary questions addressed. (c) identified gaps in the fragmentation components studied. (d) Other methodological issues.

(a) Issues of biological focus		
Identified Gap	Suggestions	Example of study or conceptual reference
Lack of studies on aquatic systems	Need for freshwater and marine experimental platforms. Need for work at the interface between aquatic and terrestrial realms and how varying fragmentation between the two realms affects arthropods persistence	[25]
Studies mainly focused on certain taxa	Need for studies on lesser studied insects, e.g. Ephemeroptera, Odonata and Trichoptera which have complex aquatic/terrestrial life cycles. Need for investigations in forgotten arthropods like e.g. Myriapoda, Pycnogonida	[41]
Lack of studies on species interactions and cascading effects	More approaches in semi-natural systems with controlled communities can allow to better understand how e.g. effects of fragmentation on one species affect other species through cascading effects	[42]
Studies mainly focused on adults	Need for understanding of effects at different life stages, particularly for species with complex life cycles	[25]
Lack of studies on model organisms	Need for building on long-lasting models like <i>Drosophila</i> species to access mechanistic understanding of fragmentation effects	[23,24,43]

(b) Issues of eco-evolutionary questions addressed		
Identified Gap	Suggestions	Example of study or conceptual reference
Lack of ecosystem studies	Study how arthropod response to fragmentation affect ecosystem functions (e.g. soil decomposition, nutrient transfer, ecosystem respiration)	[44]
Lack of studies on species interactions	Need for more small community studies where researchers track the effect of fragmentation on interaction strength. Particularly, need for studies on species competition	[45]
Lack of studies on descriptors other than abundance and community structure	Studies often focus on species richness while species respond differently to fragmentation, need for more studies on species traits as predictors to sensitivity to fragmentation	[46]
Lack of studies on species traits	Need for studies on phenotypic trade-offs or syndromes to assess the constraints of trait response to fragmentation	[47]
Lack of studies at the (epi)genetic level	Need for developing monitoring of (epi)genetic diversity change in experiments. Need for omics to unravel the (epi)genetic bases of response to fragmentation	[34]
Lack of studies on (meta)-population and community dynamics (often temporal snapshots)	Need for temporal monitoring of populations and communities, ideally with individual monitoring and information on survival/reproduction/dispersal rates	[27,29]
No studies on eco-evolutionary dynamics	Need for experimental designs deciphering the respective effects of evolutionary processes. Include common gardens and control without fragmentation in designs	[34]
Dispersal and movement often confounded	Need for clarification of the processes studied	none

(c) Issues of fragmentation components studied		
Identified Gap	Suggestions	Example study or conceptual reference
Lack of studies on matrix resistance	The quality of the matrix is mainly tackled through the presence of corridors, need for more studies on matrix quality gradients	[27]
Lack of studies on patch number	The mere effect of patch number remains poorly tackled. Develop designs where patch number varies independently of habitat amount	[48]
Lack of interactions with other components of global change	Need for studies combining e.g. climate change and pollution with fragmentation	[23,49]
Few levels of habitat fragmentation	Need for studies with higher number of levels than just continuous vs fragmented, i.e. continuous number of fragmentation levels	[50]
Not enough ecological replication	Need for more replicates at the landscape level in the design. Need for more biological replicates when relevant and for more long-term systems in different biomes	[30]
Not enough long-term studies	Need for more long-term experiment, and more time series to have the dynamics of the meta-populations, -communities, and -ecosystems on the long term	[3]
Lack of studies on random vs non-random dispersal	Studies manipulating dispersal as a proxy of connectivity often do not take into account the potential for dispersal to be non-random	[34]

(d) Other methodological issues		
Identified Gap	Suggestions	Example of study or conceptual reference
Few microcosm/mecocosm studies	Micro/mesocosms offer more control and replication particularly for complex eco-evolutionary designs, relevant for studies requiring biological reshuffling	[51]
Lack of comparability between study results	<ul style="list-style-type: none"> - Use effect sizes - report time in calendar days as well as in generation time when possible - use the same protocols to calculate traits linked to morphology, feeding, life history, physiology or behaviour - report numerical abundance as well as density per m² 	[52]
Not enough information on taxa	<ul style="list-style-type: none"> - always specify order and family of the described species - follow the ARRIVE guidelines for reporting studies on animals 	[53]
Not link with theoretical models	Build fragmentation experiments to validate theoretical predictions. Develop mixed approaches where model can help interpreting results. Feed existing models with measured parameters	[48]

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