

# 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.

## Addresses

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## Introduction

Habitat loss and fragmentation profoundly alter biodiversity [1], although some debated data recently suggested potential benefits of fragmentation *per se* [2<sup>\*\*</sup>,3<sup>\*\*</sup>,4<sup>\*\*</sup>]. 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 Ref. [14]), which might be especially relevant given the dire predictions for future habitat degradation [15]. Such a 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<sup>\*\*</sup>]. While ‘natural experiments’ (sensu Diamond [16], i.e. field observations) escape spatio-temporal scale issues and benefit from higher realism and applicability, laboratory and field manipulative experiments [17] allow to disentangle 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<sup>\*\*</sup>,21].

We created a database 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 metacommunity type` (see Supplement for exact search), yielding 5865 articles, of which 212 were finally included (Figure 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 (Figure 1a). The most investigated insect orders were Coleoptera, Hymenoptera, Lepidoptera and Hemiptera, and the most investigated non-insect classes were Arachnida and Malacostraca (Figure S2a). Formicidae, Apidae, Aphididae and Delphacidae were well represented families (Figure S2b); *Prokelisia crocea* (planthopper), *Anagrus columbi* (fairfly) and *Junonia coenia* (butterfly) were the most studied species. Surprisingly, very few studies used model species such as *Drosophila*, *Culex* or *Bombyx* (but see Refs. [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 (Figure 1, but see Ref. [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 (Figure S3b). Within species, roughly equal number of studies focused on population abundance and dispersal or movement. Fewer studies focused on other phenotypic traits, and only one study on genetics (Figure S3c). This points out a lack of

evolutionary consideration, with 1% of studies explicitly testing evolutionary processes.

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 (Figures 1a, S3c).

### Experimental settings and fragmentation components studied

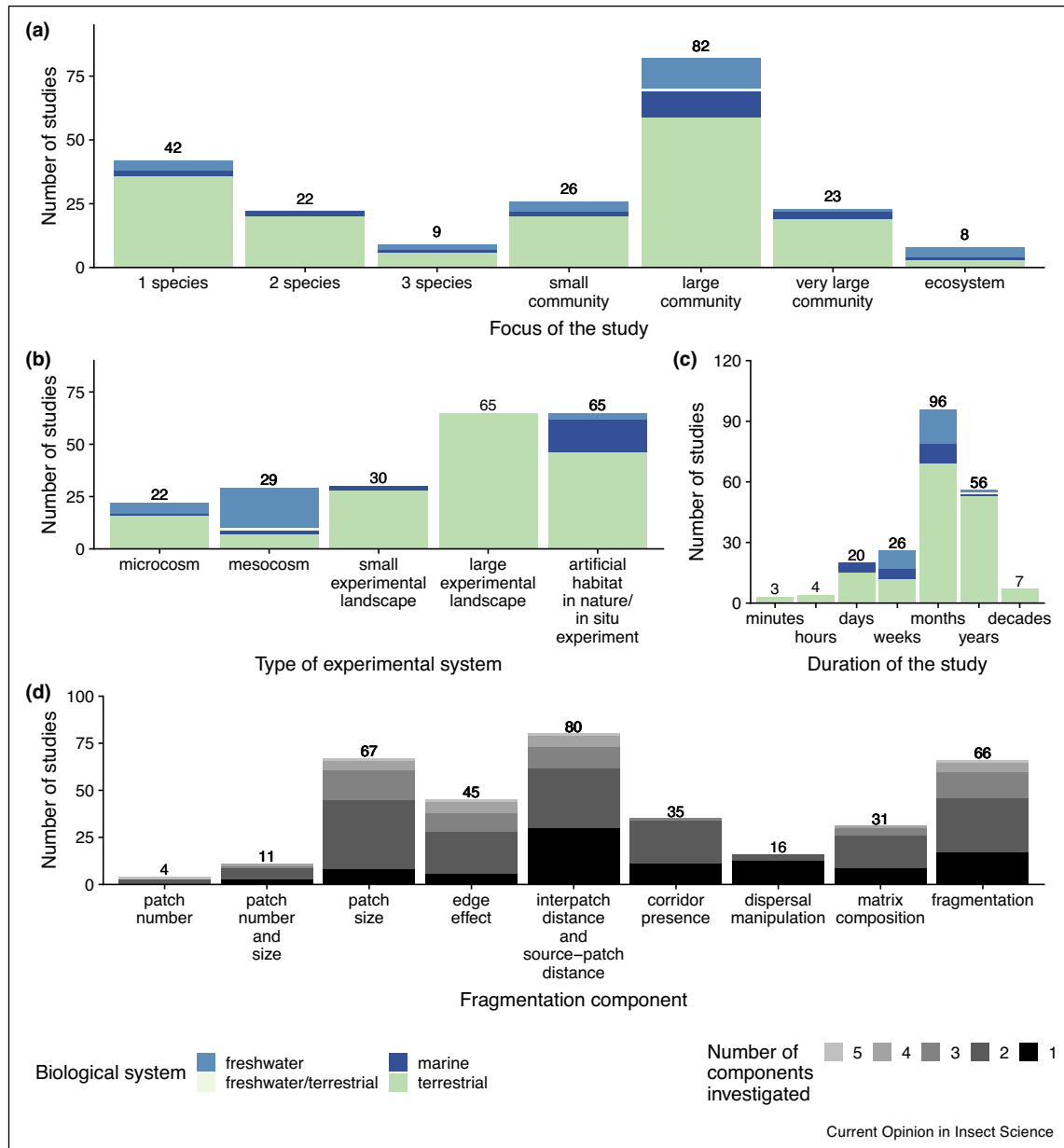
Forty-four percent of the studies made use of small or large experimental landscapes, 30% manipulated landscape features *in natura* and only 24% used microcosms or mesocosms (Figure 1b). Study duration varied from minutes to decades, but was predominantly months (Figure 1c, see supplement for discussion on generation times). Having decade-long studies such as [27,28,29\*\*] 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 two or more components (Figure 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 three levels (continuous/slightly fragmented/highly fragmented) or more (Figure 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 (Figure 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 (Figure 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

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 m<sup>2</sup>) are divided into indoor microcosms (16 studies), outdoor microcosms (1 study), and undefined (5 studies). Mesocosms (>1 m<sup>2</sup>) are divided into indoor mesocosms (3 studies) and outdoor mesocosms (26 studies). Small experimental landscapes are <1 ha, and large >1 ha (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 versus fragmented’.

experimental systems provide unique comparative power that deserves special attention. On the other hand, the low ecological replication might lead to overgeneralising 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,

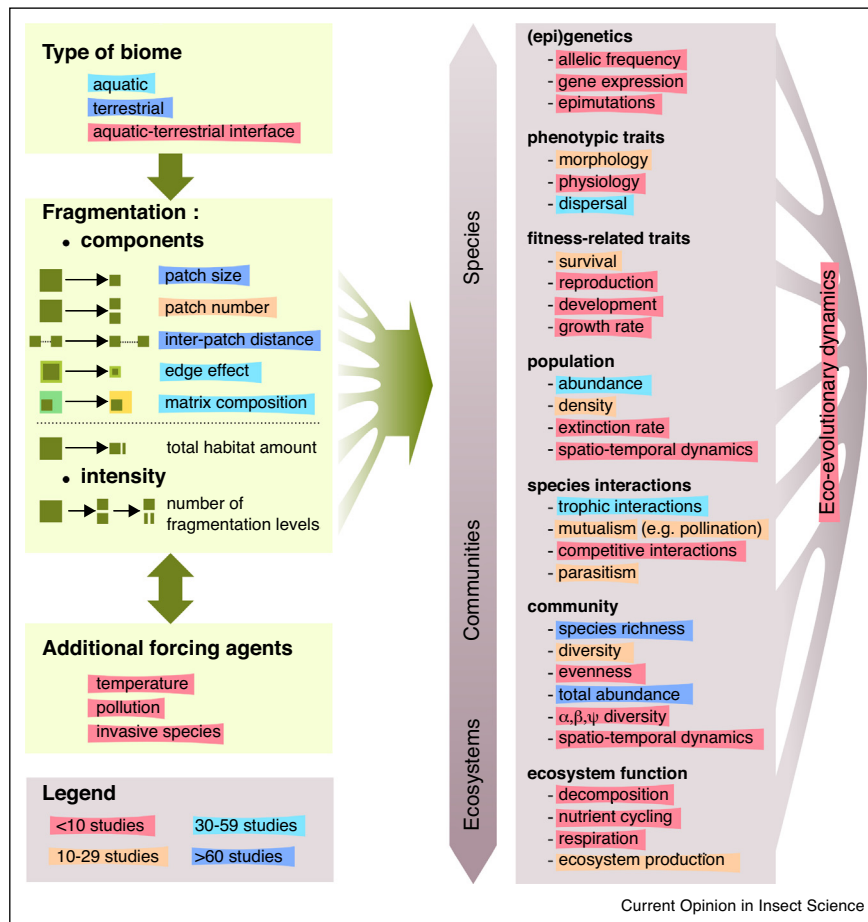
especially adding new large/small experimental systems in diverse regions and ecological biomes including at the terrestrial/aquatic interface.

**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 (Figure 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.

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 recent years for arthropods (Figure 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

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).

were pointed out as a gap 20 years ago [31] that has been partly filled since (Figure 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<sup>••</sup>]. 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 in better understanding of 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<sup>••</sup>,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 not advised to decide so, perhaps, 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<sup>••</sup>]. 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.

## Declaration of interest

The authors declare no conflict of interest.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.cois.2019.07.011>.

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