Comparing edge and fragmentation effects within seagrass communities: A meta-analysis

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Abstract

Examining community responses to habitat configuration across scales informs basic and applied models of ecosystem function. Responses to patch-scale edge effects (i.e., ecological differences between patch edges and interiors) are hypothesized to underpin the effects of landscape-scale fragmentation (i.e., mosaics of multipatch habitat and matrix). Conceptually, this appears justifiable because fragmented habitats typically have a greater proportion of edge than continuous habitats. To critically inspect whether patch-scale edge effects translate consistently (i.e., scale up) into patterns observed in fragmented landscapes, we conducted a meta-analysis on community relationships in seagrass ecosystems to synthesize evidence of edge and fragmentation effects on shoot density, faunal densities, and predation rates. We determined effect sizes by calculating log response ratios for responses within patch edges versus interiors to quantify edge effects, and fragmented versus continuous landscapes to quantify fragmentation effects. We found that both edge and fragmentation effects reduced seagrass shoot densities, although the effect of edge was statistically stronger. By contrast, fauna often exhibited higher densities in patch edges, while fragmentation responses varied directionally across taxa. Fish densities trended higher in patch edges and fragmented landscapes. Benthic fishes responded more positively than benthopelagic fishes to edge effects, although neither guild strongly responded to fragmentation. Invertebrate densities increased in patch edges and trended lower in fragmented landscapes; however, these were small effect sizes due to the offsetting responses of two dominant epifaunal guilds: decapods and smaller crustaceans. Edge and fragmentation affected predation similarly, with prey survival trending lower in patch edges and fragmented landscapes. Overall, several similarities suggested that edge effects conform with patterns of community dynamics in fragmented seagrass. However, across all metrics except fish densities, variability in fragmentation effects was twice that of edge effects. Variance patterns combined with generally stronger responses to edge than fragmentation, warrant caution in unilaterally "scaling-up" edge effects to describe fragmentation effects. Alternatively, fragmentation includes additional factors (e.g., matrix effects, patch number, mean patch size, isolation) that may enhance or offset edge effects. Fragmentation and increased edge are syndromes of habitat

degradation, therefore this analysis informs mechanistic models of community change in altered terrestrial and marine systems.

INTRODUCTION
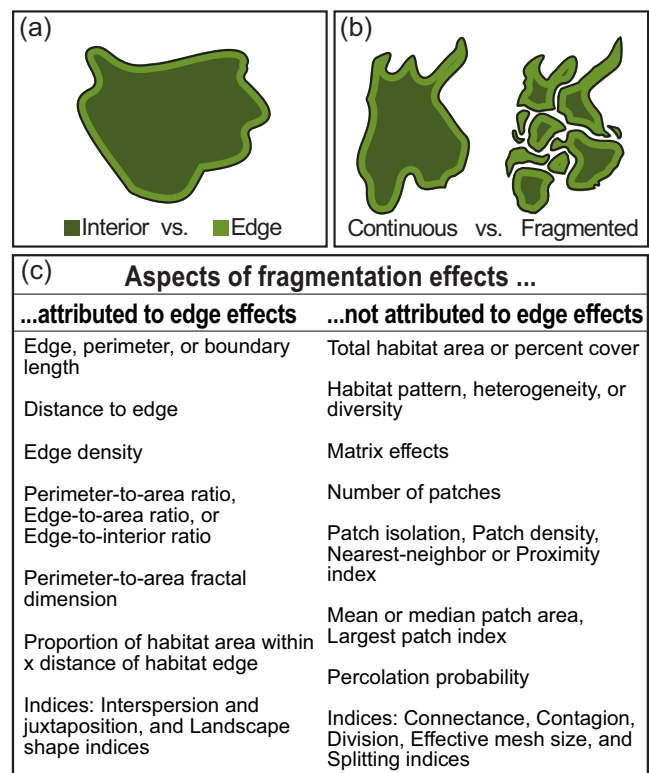
Examining patterns and mechanisms at relevant spatial scales is an essential tenet of ecological study (Levin, 1992; Wiens, 1989). However, out of logistical necessity, studies operate at feasible scales, then may implicitly or explicitly extrapolate findings to predict dynamics at other, often larger, or more spatially complex scales (McGarigal & Cushman, 2002; Morales & Ellner, 2002; Steele & Forrester, 2005). Unfortunately, ecological dynamics often do not translate across scales easily (Fahrig, 2017; Martinson & Fagan, 2014; Schmitt & Holbrook, 1990). Patterns and processes regulated by habitat configuration have been studied at multiple scales: from micro (<1 m^2) through global (Chase et al., 2020; Horinouchi, 2007). At the ambit of individual organisms, much effort has focused on faunal–habitat relationships at two nested scales: patch and landscape scales. Patch-scale studies are concerned with variables defined within a single patch (e.g., patch size, shape, gradients from patch edges to interiors), while landscape-scale studies are concerned with variables that account for across-patch dynamics (e.g., patch number, nearest neighbor distance, matrix effects) (Fahrig, 2013, 2017; McGarigal & Cushman, 2002). Therefore, the landscape-scale incorporates patch-scale variables – nested within landscapes – along with additional configuration variables. Across systems, patch and landscape studies cannot be operationally defined by any absolute scale (e.g., m^2, km^2, ha), as their sizes can vary depending on the ecosystem and taxa of interest.

Patch-scale studies often focus on edge effects by examining a gradient of ecological conditions spanning the habitat–matrix interface to the center of the habitat patch (Ries et al., 2004) (Figure 1a). Landscape-scale studies most often examine the influences of habitat area, configuration, or changes in both (Diamond, 1975; Fahrig, 2013, 2017; MacArthur & Wilson, 1967; Preston, 1960). One form of landscape alteration, fragmentation, describes the degree to which a continuous habitat is divided into more numerous, smaller patches, potentially concomitant with overall habitat loss or increases in interhabitat–matrix (Fahrig, 2003) (Figure 1b). Although habitat loss is thought to be the most important driver of fragmentation effects on communities (Andrén, 1994; Chase et al., 2020;

Fahrig, 1997), patch-scale edge effects, have also been invoked as an integral influence, particularly in driving the outcomes of fragmentation per se (i.e., the breaking apart habitat independent of area loss) (Fahrig, 2003, 2017; Haddad et al., 2015; Laurance et al., 2002, 2007; Ries et al., 2004). Although edge effects are spatially nested within fragmentation effects and have different methodologies of assessment, the two concepts have been intertwined since the coining of the term "edge effects" by Leopold (1933)

(c) **Aspects of fragmentation effects ...**	
...attributed to edge effects	**...not attributed to edge effects**
Edge, perimeter, or boundary length	Total habitat area or percent cover
Distance to edge	Habitat pattern, heterogeneity, or diversity
Edge density	Matrix effects
Perimeter-to-area ratio, Edge-to-area ratio, or Edge-to-interior ratio	Number of patches
Perimeter-to-area fractal dimension	Patch isolation, Patch density, Nearest-neighbor or Proximity index
Proportion of habitat area within x distance of habitat edge	Mean or median patch area, Largest patch index
	Percolation probability
Indices: Interspersion and juxtaposition, and Landscape shape indices	Indices: Connectance, Contagion, Division, Effective mesh size, and Splitting indices

FIGURE 1 Habitat configuration at two nested scales relevant to (a) patch-scale edge effects and (b) landscape-scale fragmentation effects. Light green is edge habitat, while dark green is interior habitat (in a and b). (c) Aspects of landscape-scale fragmentation effects on biotic responses that can or cannot been attributed to edge effects. (This is a non-exhaustive list in no particular order.) As a habitat undergoes fragmentation per se (i.e., increasing patchiness or dividing up of habitat without loss of area), edge habitat amount increases, interior habitat amount decreases, and total habitat area remains constant, all of which perhaps enhance the ecological influence of patch edges in fragmented landscapes

to describe increases in game species in "patchy" (i.e., fragmented) landscapes. The extrapolation, or "scaling-up," of edge effects to the landscape-scale appears reasonable, because as landscapes shift from continuous to fragmented configurations (Figure 1b), more patch edges are created and interiors are reduced, increasing the habitat perimeter-to-area ratio (P:A; Fahrig, 2003). Therefore, numerous synthesis studies (Haddad et al., 2015; Laurance, 2008; Laurance et al., 2002; Ries et al., 2004) have suggested that patch-scale edge effects are a key mechanism driving landscape-scale fragmentation dynamics. Furthermore, many field-based fragmentation studies rely on measurements of independent variables that can be attributed to edge effects (Figure 1c) (Carroll & Peterson, 2013; Laurance et al., 2007; Roland, 1993; Skole & Tucker, 1993). However, additional landscape-scale variables that describe habitat spatial positioning and configuration, such as patch number, mean patch size, isolation, and matrix effects (Figure 1c), may exert equal or greater influence than edge effects alone, perhaps suggesting that fragmentation and edge effects are overly entangled in the literature (Ewers & Didham, 2006; Saunders et al., 1991). Moreover, because ecological responses at any single scale can be complex, evidence that responses to related, yet distinct, and potentially scale-dependent drivers, will translate across nested scales remains equivocal (Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018).

Although habitat patch and landscape shapes can be natural, in ecosystems encroached upon by humans, edge and fragmentation effects can increase with habitat degradation as habitat spatial properties are altered (Figure 1c). Edge effects can manifest as shifts in biogenic complexity (Harper et al., 2005; Moore & Hovel, 2010), altered faunal community structure (Boström et al., 2006, 2011), increased predation (reviewed in Mahoney et al., 2018), reduced population persistence (Woodroffe & Ginsberg, 1998), and modified ecosystem functionality (Saunders et al., 1991). Fragmented landscapes, in some cases generated by human destruction, may be of poorer habitat quality for fauna relative to more continuous landscapes (of similar total area). Many observational studies have implied that high degrees of habitat fragmentation can have important negative consequences for faunal densities (Boström et al., 2011), trophic dynamics (Martinson & Fagan, 2014), species richness (Yeager et al., 2016), and extinction proneness (Laurance, 2008) across multiple biomes. Therefore, ecologists often hypothesize that both edge and fragmentation effects will yield similar and negative community responses (Fahrig, 2017).

We used seagrass meadows as a model system to conduct a quantitative meta-analysis examining edge effects and fragmentation effects on seagrass shoot density (a proxy for biogenic complexity), faunal densities, and prey survival (i.e., predation rates). We assessed whether edge and fragmentation had similar effects in direction and magnitude, to clarify the degree to which patch-scale edge effects could be extrapolated to explain landscape-scale fragmentation effects on seagrass communities. The chosen faunal response metrics represent key structural and functional components of community ecology and are therefore commonly studied across marine (Boström et al., 2006, 2011) and terrestrial systems (Haddad et al., 2015; Ries et al., 2004). Furthermore, shifts in biogenic complexity within patches (Harper et al., 2005; Moore & Hovel, 2010) and across landscapes (Byers et al., 2017; Worthington et al., 1992) are important for understanding fauna–habitat relationships (Hovel et al., 2021; Mattila et al., 2008). Therefore, the collective examination of these response metrics may elucidate mechanisms driving complex patterns, ecological processes, and community responses to habitat configuration. To further contextualize our findings, we also (1) examined the magnitude of variability in biotic responses caused by edge and fragmentation effects across studies, and (2) considered whether seagrass shoot density might be a proximate driver of faunal responses to edge and fragmentation effects.

METHODS

Literature search and meta-analysis inclusion criteria

We conducted a search using the Institute of Science Information (ISI) Web of Science, (last accessed on 13 May 2021) to gather peer-reviewed literature examining edge effects and fragmentation effects on biogenic complexity, faunal densities, and predation in seagrass ecosystems. Search terms included (1) seagrass AND (2) edge effects OR fragmentation effects AND (3) density OR predation OR survival OR mortality OR trophic interactions. We supplemented this database with additional articles known to us. All candidate studies were judged for inclusion in our meta-analysis based on the following criteria:

(1) The study was an original experiment in a mesocosm or natural setting providing edge-effect data (i.e., responses in patch edges vs. interiors) or fragmentation-effect data (i.e., responses in fragmented vs. continuous landscapes) for one or more of our response metrics of interest in extractable form (i.e., table, figure, or text). Response metrics were natural seagrass shoot density, faunal density, and

predation survival. Initially, we considered several metrics of biogenic complexity because they may respond to habitat configuration differently, yet shoot density was ultimately chosen as it was the most common metric reported. Shoot density data were only extracted from studies also examining faunal response metrics, because we were interested in examining fauna–habitat relationships in the context of proximate (e.g., shoot density) and ultimate (e.g., edge, fragmentation) drivers. For faunal density responses, if data for "nested" taxonomic levels were provided (e.g., fish, flounder), we extracted data for both levels (to be used in separate analyses, detailed below). Prey survival responses included data expressed as, or converted to, proportion survival or survival time (e.g., hours to consumption) of sessile or tethered prey. Only survival from uninhibited predator exposure was considered.

(2) The response metric(s) included the mean, sample size, and either standard error (SE), standard deviation (SD), or confidence interval (CI).

(3) Levels of edge effects (e.g., edge, interior) and fragmentation (e.g., fragmented, continuous) were typically expressed as discrete categories. Therefore, we accepted the operational definitions used by these studies, but also included metadata such as edge/interior widths and distances, and fragmentation degree in our database to illustrate the range of definitions used across studies. All included studies examined fragmentation as a state (i.e., configuration), rather than an active process (i.e., changing configuration through time). For studies that included more than two discrete levels of edge (e.g., integer distances) or fragmentation (e.g., continuous, patchy, very patchy), only the most extreme levels were included in effect size calculations (e.g., the distances closest to the patch edge and center; the most continuous and fragmented landscape classifications).

Figure data were extracted using DataThief III software (Tummers, 2006).

Our literature search yielded 43 articles that met our criteria, consisting of 27 edge-effect studies and 20 fragmentation-effect studies, with four examining both effects (Appendix S1: Table S1). Articles were biased geographically toward North America ($n = 25$), followed by the Asia-Pacific region ($n = 11$), Europe ($n = 6$), and Africa ($n = 1$) (Appendix S1: Table S2). Articles were also biased toward temperate zones ($n = 26$), followed by subtropical ($n = 16$), and tropical zones ($n = 1$). Faunal density, measured as individuals per unit area or catch per unit effort, was reported in 84% ($n = 36$) of studies, while 30% ($n = 13$) of studies provided data on prey survival or mortality (from tethering or mark-recapture experiments). Most (84%, $n = 36$) studies conducted experiments in natural seagrass (as opposed to artificial), and 42% ($n = 15$) of those studies provided shoot density data. Most edge-effect studies defined edges similarly (0–2 m from the interface) while interior definitions included a wider range of distances (2–60 m from the interface) or simply defined the interior as the patch center (Appendix S1: Table S2). Edge-effect studies also included a wide range of patch sizes for natural seagrass (3-m^2 to 60,980-m^2) and a small range for artificial seagrass (0.0625-m^2 to 17-m^2). Fragmentation studies included a wide range of landscape sizes for natural seagrass (100-m^2 to 0.6-km^2) and a small range for artificial seagrass (0.0625-m^2 to 9-m^2) (Appendix S1: Table S2). Fragmentation studies using small artificial seagrass landscapes examined small crustacean epifauna, which are likely to respond to ecological processes on spatial scales matching the experimental scale (Kotliar & Wiens, 1990). Furthermore, most studies included justification for their edge/interior definitions or landscape area relevant to their experimental design (i.e., discrete patches/landscapes available in their system, feasible replicate plot areas) or target taxa (i.e., ambit of habitat utilization).

Calculating log response ratios

To quantify edge and fragmentation effects across studies, we calculated log response ratios (LRR) using methods described by Hedges et al. (1999) within the R computing environment (v.4.1.0; R Core Team, 2021). Experimental log response ratios (LRR$_i$) were

$$\ln\left(\frac{\overline{X}_e}{\overline{X}_i}\right) \text{ or } \ln\left(\frac{\overline{X}_f}{\overline{X}_c}\right) \quad (1)$$

the ratio of the mean response in patch edges ($\overline{X}_e$) or fragmented landscapes ($\overline{X}_f$) over the mean response in patch interiors ($\overline{X}_i$) or continuous landscapes ($\overline{X}_c$), respectively. A positive LRR$_i$ indicates a relative increase in response within edge or fragmented habitats versus interior or continuous habitats, respectively. Conversely, a negative LRR$_i$ indicates the relative decrease in response within edge or fragmented habitats versus interior or continuous habitats, respectively.

Our database included a total sample size (k) of 338 unique LRR$_i$ across the 43 studies. We pooled non-independent time or spatial replicates using methods described by Hedges et al. (1999) (Appendix S2: Section S1). To assess statistical clarity of differences in response metric effect sizes between edge and fragmentation studies (i.e., "study type"), we used mixed

effects (ME) models (*sensu* Hughes et al., 2004) with the "rma.mv" function from the *metafor* package in R (Viechtbauer, 2010). For each response metric, LRR_i was the response variable and study type (i.e., edge-effect study, fragmentation-effect study) was the fixed effect. Within- and among-experiment variance were accounted for through the inclusion of a sampling error term (v_i) (Appendix S2: Section S1), and study identity as a random intercept, respectively. Including this random intercept accounts for non-independence of multiple effect sizes from a single study (Cameron et al., 2016). In addition, for each response metric, we performed a random effects (RE) model on each study type, separately, to determine if the edge-effect or fragmentation-effect LRR differed from zero. We obtained the mean LRR and 95% CI from RE models, which included v_i and a study identity random intercept using the "rma.mv" function (*metafor*; Viechtbauer, 2010).

Faunal density LRRs were examined for several taxa (i.e., total fauna, total fish, total invertebrates) and guilds (i.e., benthic fish, benthopelagic fish, epifaunal invertebrates, infaunal invertebrates). If a single study provided data for nested taxonomic levels (e.g., "fish" vs. multiple fish species), we calculated LRR_i for the lowest taxonomic levels (i.e., individual species) to allow for taxa/guild divisions. A few studies identified guilds, such as "nekton," "macroinvertebrates," or "fish," which could not be divided into more specific taxonomic/guild designations, but were included in the appropriate board taxa effect sizes. Taxa and guild LRRs were used to explore differences in faunal ambit driven by traits such as life history, body size, and mobility that determined the grain and extent of habitat heterogeneity to which an animal can respond (Kotliar & Wiens, 1990). As supplemental analyses, we also explored LRRs for more specific taxa/guilds, which were reported in at least two studies of each type (i.e., edge, fragmentation) but typically had lower sample sizes. These taxa/guilds were: perciformes, sygnathiformes, decapods, blue crabs (*Callinectes sapidus*; the single most studied species), gastropods, and small crustaceans (i.e., amphipods, isopods, copepods, ostracods, mysids).

To explore the role of commonly reported study descriptors (i.e., seagrass species, natural vs. artificial seagrass, global region, broad taxa/guild), we included them as fixed factors in additional ME models of LRR for each study type (rma.mv, *metafor*; Viechtbauer, 2010). Studies did not provide a uniform data set of habitat configuration definitions (i.e., edge/interior distances, fragmentation degree), therefore these descriptors were not included in ME models. We were interested in whether ME models would account for additional heterogeneity in LRRs (i.e., tighten the CIs) compared with the

RE models (ME models are further described in Appendix S2: Section S2). A comparison of the LRRs and CIs estimated by each of the RE and ME models (Appendix S1: Figure S1) revealed that our results were highly robust to the LRR estimation method used. For simplicity, we present a uniform, comparable set of RE model-estimated LRRs (Viechtbauer, 2010, 2020). We focus our results on nine response metrics: shoot density, seven faunal taxa/guild densities, and invertebrate prey survival in the context of both edge and fragmentation effects. Invertebrate prey included decapods, bivalves, and sea urchins; sample sizes were too small for taxon-specific examinations of survival. One additional LRR for edge effects on prey survival (of both fishes and invertebrates) was included as a supplemental analysis because no fish prey was used in fragmentation studies (Appendix S1: Table S3).

Relative magnitudes of variability in biotic responses to edge and fragmentation effects were determined for each response metric by directly comparing RE model estimates of tau squared (τ^2), for the two study types. τ^2 is the common metric used in meta-analysis to describe the amount of variance among observed effects in different studies (i.e., between-study variance) and therefore is used to reflect the variance of the "true" effect size (Borenstein et al., 2009). (In contrast, CIs indicate with 95% certainty that the "true" effect size falls within the interval.)

Shoot density as a correlate of edge or fragmentation effects on fauna

We examined the influence of seagrass shoot density on faunal responses in edge-effect and fragmentation-effect studies in two ways. First, as a supplemental exploration, we qualitatively summarized shoot density–fauna response relationships analyzed or discussed in 17 studies. Second, for 15 studies (not fully coinciding with the preceding analysis) that provided paired shoot density and taxon-specific (i.e., fish, invertebrate) response measurements, we used Pearson pairwise correlation to quantitatively determine if shoot density explained fish density, invertebrate density, or invertebrate prey survival. Correlation analyses were separated by study type (i.e., edge, fragmentation) to preserve inherent sampling differences (i.e., edge and interior samples vs. haphazard sampling in continuous and fragmented landscapes). Sample sizes for each correlation were determined by the number of paired shoot density (i.e., cores, quadrats) and faunal response (e.g., core, quadrat, transect, predation assay) measurements. To ensure data independence, if multiple taxon-specific densities (e.g., several fish species) were

reported with a single shoot density, we averaged the faunal densities, or if provided, we used data from a higher taxonomic level (e.g., "fish density"). We compared shoot densities ($\log_{10}$ shoots m^{-2}) to each of the fish and invertebrate densities ($\log_{10}$ no. m^{-2}) for both study types. Invertebrate prey survival was typically reported differently in these edge and fragmentation-effect studies (i.e., the subset of studies providing paired survival and shoot density data); therefore, we analyzed the most reported metric for each. Specifically, we correlated shoot density to survival time ($\log_{10}$ min) in edge studies, and to proportion survival (arcsine square-root transformed) in fragmentation studies.

RESULTS

Seagrass shoot density was 19% greater (CI did not include an LRR of zero) in patch interiors than edges (percentages are back-transformed LRRs; LRR and CI values are given in Appendix S1: Table S3). In addition, shoot density trended 13% higher (CI included zero) in continuous than fragmented landscapes (Figure 2). Mean LRRs for edge and fragmentation effects on shoot densities were not significantly different ($Q_M = 1.31$, df $= 1$, $p = 0.253$). In contrast, total faunal density was 23% higher in patch edges and trended 5% higher (CI included zero) in fragmented landscapes, despite the relative decrease in seagrass shoot density in these same contexts (Figure 2). Mean LRRs of edge and fragmentation effects on total faunal density were statistically different ($Q_M = 109.789$, df $= 1$, $p < 0.001$).

Total fish density had similar LRRs ($Q_M = 0.02$, df $= 1$, $p = 0.886$) and zero-including CIs for edge and fragmentation effects: trending 26% higher in patch edges (vs. interiors) and 44% in fragmented (vs. continuous) landscapes (Figure 2). Division of fishes by guild revealed that benthic fish density was 125% higher at patch edges, yet trended 22% lower (CI included zero) in fragmentation landscapes, and mean LRRs across-patch and landscape scales statistically differed ($Q_M = 7.06$, df $= 1$, $p = 0.008$). Alternatively, benthopelagic fish densities had weak (CIs included zero) and similar responses ($Q_M = 0.01$, df $= 1$, $p = 0.934$), with density trending higher by 3% in patch edges and 44% in fragmented landscapes (Figure 2).

In contrast with total fish density, mean LRRs for total invertebrate density were dissimilar in edge and fragmentation studies ($Q_M = 126.91$, df $= 1$, $p < 0.001$). Invertebrate density was 24% greater in patch edges, yet trended 19% lower (CI included zero) in fragmented landscapes (Figure 2). The total invertebrate density response was heavily influenced by the subset of epifaunal
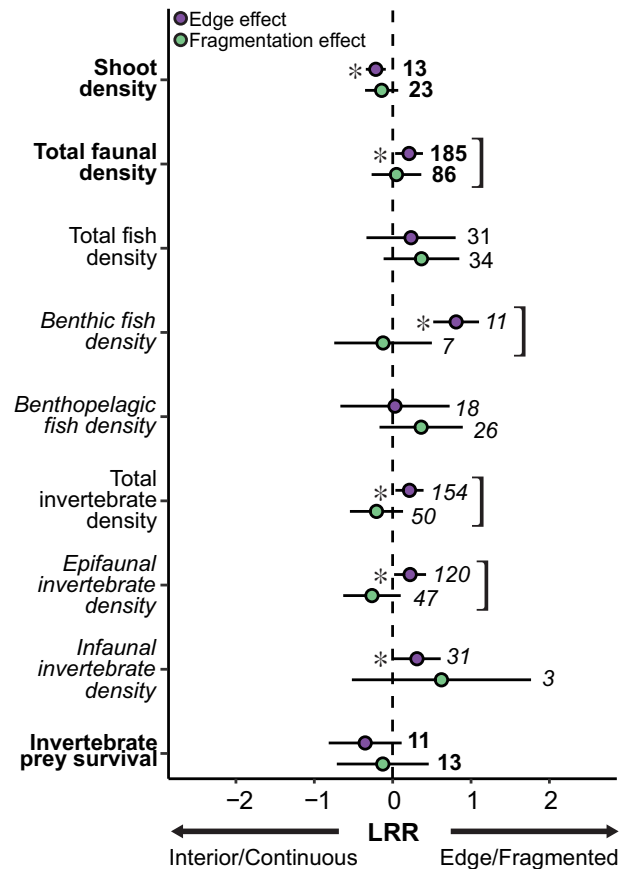
FIGURE 2 Mean log response ratios (LRR) for edge and fragmentation effects on response metrics. Error bars are 95% CIs with sample sizes (k) of comparisons (LRR$_i$) and significance from zero (*). Bold response metric k sum to 331. Total $k = 338$ (fish prey survival, $k = 7$ only included in Appendix S1: Table S3). The two taxa groups in normal font (fish and invertebrates) are subsets of "Total faunal density." Italic font depicts two guild subcategories of the preceding taxa groups. Brackets (]) indicate differences ($p < 0.05$) between edge and fragmentation studies for a given response metric. A positive mean LRR indicates a relatively higher response in patch edges versus interiors and fragmented versus continuous landscapes. A negative mean LRR indicates a relatively higher response in patch interiors versus edges and continuous versus fragmented landscapes

invertebrates, which also strongly responded to edge but not fragmentation effects, giving statistically different mean LRRs ($Q_M = 129.01$, df $= 1$, $p < 0.001$). Epifaunal invertebrate density was 25% higher in patch edges and trended 23% lower (CI included zero) in fragmented landscapes. However, infaunal invertebrate responses to edge and fragmentation were statistically similar ($Q_M = 0.63$, df $= 1$, $p = 0.427$), with density 36% higher in patch edges and trending 86% higher (CI included zero) in fragmented landscapes (Figure 2).

Invertebrate prey survival was not consistently influenced by edge or fragmentation effects and LRRs

were not statistically different from each other ($Q_M = 0.28$, df = 1, $p = 0.596$): trending 30% lower in patch edges and 22% lower in fragmented landscapes (both with CIs including zero; Figure 2). Three edge-effect studies examined fish prey survival ($k = 7$). When fish were included in the edge-effect LRR, similar results were observed with 24% lower prey survival in patch edges (Appendix S1: Table S3).

A direct comparison of the τ^2 of the mean LRR for each response metric (Figure 3) revealed that responses to fragmentation effects were often more variable than responses to edge effects. Fragmentation effects on both shoot density and infaunal density (acknowledging low k) yielded >4 times more variability than edge effects. Similarly, fragmentation effects on most other response metrics had a $\tau^2 \geq 2$ times those of the corresponding edge-effect responses. Two notable exceptions were the nested responses of total fish and benthopelagic fish densities, which each had roughly 1.5 times more variability in edge than fragmentation effects (Figure 3). The relatively greater variability in fish density responses to edge than fragmentation effects is primarily driven by benthopelagic fishes, yet we also note that benthic fish density responses had extremely small (and therefore

relatively similar) edge and fragmentation effects τ^2 (Figure 3).

Shoot density influences on faunal responses

Both our supplemental qualitative analysis (Appendix S1: Table S4) and quantitative correlation analyses of shoot density–faunal response relationships revealed a mixture of relationship strengths and directions. Fish densities in two edge-effect studies were negatively correlated with seagrass shoot densities ($r = -0.78$, df = 9, $p = 0.004$). Only one fragmentation study provided (two) paired fish–shoot density measurements, so no correlation was examined for these data. By contrast, patterns in invertebrate density were not well explained by shoot density in either five edge-effect studies ($r = -0.12$, df = 38, $p = 0.469$) or four fragmentation-effect studies ($r = -0.10$, df = 30, $p = 0.594$). Similarly, no strong correlation was seen between invertebrate prey survival and shoot density in two edge-effect studies ($r = 0.55$, df = 4, $p = 0.263$) or six fragmentation-effect studies ($r = 0.13$, df = 18, $p = 0.575$).
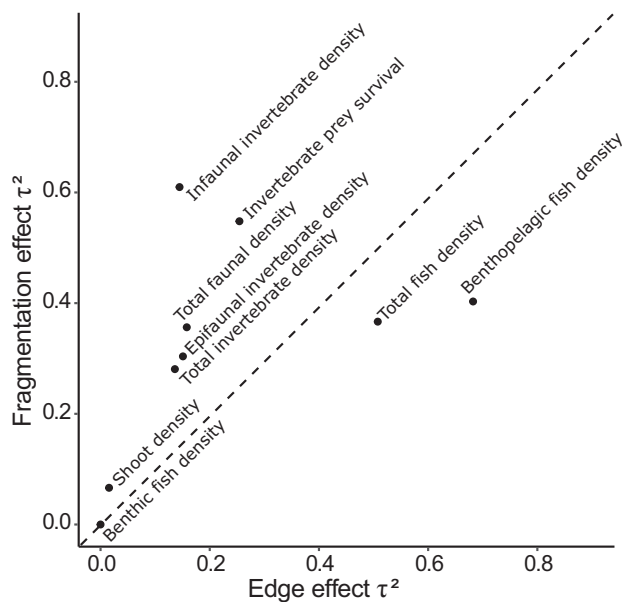
FIGURE 3 A direct comparison of the total heterogeneity (τ^2) of the true effects sizes of biotic responses to edge and fragmentation effects. For each response metric (black dots; k given in Figure 2), the edge-effect τ^2 is the x-coordinate, while fragmentation-effect τ^2 is the y-coordinate. The dashed line is a $y = x$ reference line. Points above the dashed line have more heterogeneity in response to fragmentation than edge effects. Points below the dashed line have more heterogeneity in response to edge effects than fragmentation

DISCUSSION

Patterns within seagrass ecosystems revealed several important considerations regarding the extrapolation of habitat influences across scales to explain community responses. Across most response metrics, it appears that edge effects can be useful in predicting community dynamics in fragmented landscapes. Indeed, edge and fragmentation effects often had similar, relatively small magnitude (compared with variability), mean impacts on seagrass shoot density, faunal densities, and prey survival. However, across taxa and guilds, densities responded more consistently positively to edge than fragmentation effects, while shoot densities responded negatively to both effects. Moreover, patterns of variability distinguished patch and landscape scales, as responses to fragmentation consistently exhibited greater variability (τ^2) than did edge effects (with the exception of nested fish densities) (Figure 3). We infer that edge effects are a core component of fragmentation dynamics, but additional interpatch variables inherent in fragmented habitats, such as matrix arrangement or quality, as well as patch number, size, and isolation, generate added variability in landscape-scale studies (Ewers & Didham, 2006; Fahrig, 2017). Furthermore, differences among various underlying natural and anthropogenic causes of

fragmentation can manipulate and therefore create variation in community responses to fragmentation (Laurance, 2008).

Edge effects, and the relative amount of edge habitat within a landscape may, in part, determine faunal responses to fragmentation. Total faunal density-effect sizes were small and positive, yet fauna often responded stronger to edge than fragmentation effects (Figure 2). For instance, total invertebrate density exhibited a significantly positive response to edge effects, mostly driven by the subset of epifaunal invertebrate responses ($k = 120$), and secondarily driven by the subset of infaunal invertebrate responses ($k = 31$) (Figure 2). Furthermore, the total invertebrate response to fragmentation was statistically different from the edge-effect response (although not from zero) and trended negatively (Figure 2). This difference in edge and fragmentation responses may stem from the pooling of differing fragmentation responses across guilds (i.e., epifauna, infauna) and differing responses among commonly sampled epifaunal taxa/guilds (namely decapods and small crustaceans) (Appendix S1: Figure S2).

A large portion of epifaunal invertebrates were small crustaceans, which exhibited a strong positive density response to edge effects and a weaker positive response to fragmentation (Appendix S1: Figure S2). These patterns may be partially explained by "settlement shadows" (Orth, 1992), or water flow dynamics, which cause more fauna to settle into seagrass edges, while reduced flow and settler concentration farther into seagrass decrease settlement toward patch interiors. However, across multiple patches, additional landscape-scale configuration features are likely to introduce further variability in the underlying mechanisms determining faunal distributions. The next most commonly sampled epifaunal taxon, decapods (including blue crabs), trended negatively (although CIs included zero) in response to both edge and fragmentation effects (Appendix S1: Figure S2). Decapods and blue crabs, in particular, may rely heavily on higher seagrass shoot density for predation refuge (Hovel & Fonseca, 2005) especially from fish predators (Mahoney et al., 2018). The uneven sampling across study types of decapods and small crustaceans, which have offsetting responses to both effects, in part accounts for the statistical and directional differences in total and epifaunal invertebrate density LRRs (Figure 2).

Total fish densities were elevated in both patch edges and fragmented landscapes (both with CIs including zero), potentially responding to higher invertebrate prey (e.g., small crustacean) availability and lower shoot densities (evinced by the negative correlation of fish and shoot densities in edge-effect studies). As in total invertebrates, the lack of statistical significance in the responses of total fish density to habitat configuration effects may

be explained by differences in responses among constituent fish guilds. Benthic (Figure 2) and slow moving, cryptic (i.e., sygnathiformes) fish densities (Appendix S1: Figure S2) may respond strongly positively to edge effects, to take advantage of the "nearest refuge" from potential predators (Bishop & Byers, 2015; Virnstein & Curran, 1986). However, relatively weaker fragmentation responses by benthic fishes indicate that edge association may not reliably scale up to landscape configuration responses due to the low dispersal abilities of these fishes (Yeager et al., 2016). In contrast, benthopelagic (Figure 2) and higher mobility (i.e., perciformes) fishes (Appendix S1: Figure S2) have been observed to readily cross mosaics of structured and unstructured habitats (Yeager et al., 2016), potentially explaining their lack of strong density response to either effect.

Faunal community distributions within seagrass are also influenced by predator–prey dynamics (Hovel & Lipcius, 2001, 2002; Yarnall & Fodrie, 2020). Both edge and fragmentation effects on invertebrate prey survival produced mean LRRs with zero-including CIs, probably due to the pooling of prey species (although all prey were immobilized) and (unidentified) predators and predation strategies. However, these mean LRRs were similar to each other (Figure 2), perhaps indicating that certain predation strategies are scale invariant in seagrass systems. At the patch scale, prey survival trended lower in edges than interiors, supporting the hypothesis that predators patrol patch edges in search of prey (Carroll & Peterson, 2013; Mahoney et al., 2018). Similarly, we found lower mean prey survival in fragmented than continuous landscapes, suggesting that predators use matrix corridors in fragmented landscapes to facilitate edge patrolling and movement among patches (Hovel & Lipcius, 2002; Irlandi et al., 1995). Additionally, along patch edges and within fragmented landscapes, relatively lower shoot densities and higher faunal densities (Figure 2) may increase predator–prey encounter rates (Hovel & Lipcius, 2001; Norbury & Overmeire, 2019), creating hotspots for trophic transfer. Notably, however, fragmentation effects on prey survival were ≥50% more variable than edge effects (Figure 3). The additional variability in fragmentation effects on prey survival (i.e., predation rates) may be produced by interpatch variables. Among fragmented landscapes, smaller mean patch sizes may reduce the proportion of patches occupied by higher trophic levels (Komonen et al., 2000). Furthermore, higher mean patch isolation may increase predator foraging effort and reduce predator movement among distant patches (Fodrie et al., 2015; Hovel & Lipcius, 2001; Martinson & Fagan, 2014; Micheli & Peterson, 1999).

Across biomes, positive relationships between fine-scale biogenic complexity and each of faunal density and

prey survival are fundamental to our understanding of natural systems (Hovel & Lipcius, 2002; Mattila et al., 2008; Norbury & Overmeire, 2019). However, our study indicated that seagrass shoot density and total faunal density are negatively related in the context of edge effects (evinced by non-overlapping CIs; Figure 2). Furthermore, our correlation analyses and summarization of shoot density–faunal response relationships across studies (Appendix S1: Table S4) found a mix of relationship strengths and directions. The lack of consistent, positive relationships across scales, potentially dampened by interactions with covariates such as distance from edge (Moore & Hovel, 2010) or patch size (Horinouchi, 2007), suggests that extrapolation of biogenic complexity to predict faunal responses, may not be applicable at mismatched absolute sampling scales (e.g., quadrat sample vs. transect survey) (Worthington et al., 1992). Furthermore sampling of shoot density and faunal responses at large matching scales may elucidate whether biogenic complexity is an intermediate driver of seagrass edge or fragmentation effects.

Habitat perimeter-to-area (P:A) ratio is commonly implied to bridge spatial scales and to justify the extrapolation of edge effects to explain fragmentation effects (Haddad et al., 2015; Laurance, 2008; Ries et al., 2004). Few studies in our meta-analysis reported this variable, which prevented us from quantitatively assessing the P:A ratio as a common predictor of edge and fragmentation effects. Regardless, we assert that, while the P:A ratio geometrically applies to both patch and landscape scales and may be cautiously used to scale up edge effects to partly explain fragmentation effects (Carroll & Peterson, 2013), it does not account for additional landscape-scale attributes (Figure 1c) that probably underpin the added variability in fragmentation versus edge effects (Figure 3). Therefore, the combined examination of edge effects and interpatch variables better explains the biotic responses to fragmentation (Ewers & Didham, 2006; Saunders et al., 1991).

Our findings highlight critical opportunities for further exploration of relationships between taxon-specific densities or complex processes (e.g., predation) and seagrass habitat configuration at multiple scales (e.g., within patch, among patch, across landscapes) (Hovel et al., 2021). Our meta-analysis illustrates that seagrass community responses to edge effects may help to explain responses to fragmentation, yet we caution investigators against assumptions that edge and fragmentation effects are functionally equivalent. In fact, several faunal densities have shown, statistically and potentially ecologically, different mean responses to edge and fragmentation. Moreover, a direct comparison of the variability in edge and fragmentation effects (Figure 3) illustrated that fragmentation studies often yield more variable results than edge-effect studies. This is probably because, in fragmentation studies, variability in taxon-specific fauna–habitat relationships is further compounded by responses to numerous landscape-scale features, such as matrix effects, patch number, size, and isolation. This form of comparative meta-analysis appears particularly important in systems experiencing human-driven alteration, such as terrestrial forests (Skole & Tucker, 1993), for which the extrapolation of edge effects to explain fragmentation has been encouraged (Ries et al., 2004). Coastal marine habitats are also experiencing degradation (Boström et al., 2011) and are typically orders of magnitude smaller in absolute area than terrestrial analogs, for which multiscale studies are more difficult. Therefore, examining configuration at multiple nested scales appears particularly tractable in model seagrass, reef, saltmarsh, and mangrove forest systems as a key direction for future work to advance our understanding of the scale dependence of drivers organizing faunal communities.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Yarnall et al., 2021) are available from the Biological and Chemical Oceanography Data Management Office at: https://doi.org/10.26008/1912/bco-dmo.864783.1

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