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Saltmarsh resilience controlled by patch size and plant density of habitat-forming species that trap shells

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HIGHLIGHTS

• Invasive cordgrass and shell debris are two of the ecosystem engineers.
• Patch size of remnants, plant density and multitude of shell aggregations along patch edge show positive interactions.
• Large patches with denser plants trap more shells along patch edges where they decrease erosion.
• Small patches with lesser denser plants cannot persist as trapping more shells at interior locations where they hinder plant re-growth.
• The ecosystem collapses while the patch size are below ~20m².

GRAPHICAL ABSTRACT

Habitat fragmentation into small patches is regarded as a vital cause of biodiversity loss. Fragmentation of habitat-forming species is especially harmful, as patchiness of such species often controls ecosystem stability and resilience by density and patch size-dependent self-reinforcing feedbacks. Although fragmentation is expected to weaken or even break such feedbacks, it remains unclear how the resulting patchiness of habitat-forming species affect ecosystem resilience to environmental stresses. Here, using Spartian alterniflora, the habitat-forming species in saltmarshes as a model, we investigate how patch size, plant density, and shell aggregation interactively control the persistence of a degrading salt marsh that suffered from erosion induced by hydrodynamics. Our results demonstrate that large patches can trap more shells along the patch edge than the smaller ones, therefore significantly facilitating plant re-growth within the patch. Shell removal experiments further reveal that large patches trapping more shells along patch edges reinforce their own persistence by decreasing erosion and thus facilitating plant recovery. By contrast, small patches with lesser plants cannot persist as they trap less shells along patch edges but are able to accumulate more shells at interior locations where they hinder plant re-growth, indicating a critical
1. Introduction

Unprecedented anthropogenically-driven environmental changes are progressively impacting the functioning and biodiversity of terrestrial and aquatic ecosystems (Lejeune et al. 2010; Jeppesen et al. 2015). Increasing evidence emphasizes that individual species decline as a result of a suite of threats including global warming-related climatic changes, pollution, and habitat destruction and degradation that may often act in concert (Kenedy et al. 2002; Gadelha 2015; Claar 2018). A major consequence of habitat destruction is that it often yields a landscape of much smaller and isolated patches of key habitats, this in turn typically negatively impacts biodiversity as the amount of suitable habitat available to organisms is reduced and exchange of individual of propagules between patches is often hampered.

Habitat degradation may be particularly harmful when ecosystem functioning and services depends on habitat-forming species that generate self-reinforcing feedbacks. For example, desert plants, dune grasses, seagrasses, and salt marsh plants facilitate themselves and many associated species by ameliorating physical stress in the hostile environments in which they grow (Mucina et al. 2006; Gardner 2016). However, as the strength of this self-facilitation typically depends on patch size and density, habitat fragmentation can weaken or break these critical feedback interactions, causing a sudden collapse of the ecosystem (Maxwell et al. 2017). Yet, despite the large potential ecological and economic implications of such ecosystem collapse, it remains unclear how habitat fragmentation and the resulting patchiness affect the ability of these systems to resist environmental stresses and thus to underpin ecosystem persistence.

Using salt marshes as a model system, we investigate how patch size, plant density, and shell aggregation interactively control the persistence of a degrading salt marsh. Saltmarsh ecosystems are vital components of coastal ecosystems worldwide, providing important ecosystem services including carbon storage and nutrient filtration, biodiversity and fisheries enhancement, and coastal shoreline protection (Hale et al. 2009; Barbier et al. 2011; Perkins et al. 2015). Human influence has led to the massive reduction of salt marshes, more than 30% of which are lost or degraded worldwide. Importantly, degrading marshes can collapse rather suddenly, with the habitat-forming plants such as cordgrasses falling apart into patches that may often progressively decline in size as the marsh continues to degrade (Lopez et al. 2014). Mounting evidence demonstrates that the extent to which salt marsh vegetation can facilitate its own growth and survival by shaping its landscape through water flow attenuation, particle trapping and sediment stabilization, strongly depends on patch size and plant density (Bouma et al. 2009; Willemsen et al. 2016; Reijers et al. 2020). Yet, although this implies that salt marshes fragmentation directly feeds back to the marsh plants’ habitat-forming and thus overall marsh stability and persistence, the role of this processes in habitat loss remains poorly understood.

In the Yellow River Delta, extreme storm surge has caused habitat fragmentation of Spartina alterniflora, a pioneer dominant, invasive cordgrass, with resulting in patchiness of this marsh-forming habitat (Ma et al. 2019). Coincident with these changes, anthropogenically-driven environmental modifications have contributed to a vast number of shell productions, which are the major components of death assemblages, exhibiting extensive local tidal flats covered with empty mollusc shells (Yan et al. 2020). The cordgrass patches in turn trap this shell debris, where it is fixed in the sediment layer between the root mat of the plants. Prior studies suggested that shell aggregation introduced complexity and heterogeneity into environments and can be important in mediating ecosystem resilience by affecting population-, community- and ecosystem-level processes (Gutiérrez and Iribarne 1999; Lenihan 1999; Gutiérrez et al. 2003). The magnitude of their controls and ecological consequences depends on their interplay with the environment where shell aggregation takes place (Gutiérrez et al. 2003). Therefore, although patchiness of habitat-forming species often controls ecosystem stability and resilience, the mechanisms underlying patch-level persistence to physical stress remain poorly understood.

To test our hypothesis, we adopted both field surveys across a range of patch sizes and manipulative experiment with shells removal, to test the interactive effects of shell aggregation, plant density and patch size on patch stability and plant re-growth. We hypothesized that the eco-hydrological interaction determining the plant growth depends on patch properties, in turn, the new vegetative or structural biomass would maintain, or even increase the patch stability. We specifically test that (1) the magnitude and position of shell aggregation depends on patch sizes, and there exists a threshold of patch sizes determining their shifts (2) plant density positively links to patch sizes, but differs between the position of patch edge and center and (3) shells removal can significantly impact on the patch stability by increasing patch contraction, but the magnitude depends on patch sizes. Our results may provide attempt to build a better mechanistic understanding of how the eco-hydrological interactions of patch size, shell aggregation and plant density on saltmarsh ecosystem persistence at local patch-level, thereby informing future management practice of highly degraded saltmarshes to detect this threshold of spatial isolated patches is a key step for guiding efficient restoration management.

2. Methods and materials

2.1. Study site and system

Field work was conducted in the Yellow River estuary (37°49′10.39″ N, 119°6′57.08″ E) of the Yellow River Delta National Nature Reserve, northern China (see Cui et al. 2011) for a map of the study site. The climate is temperate monsoonal climate, with an average annual precipitation of 537.3 mm and an average annual temperature of 12.88 °C (Yan et al. 2020). Tides are irregular semidiurnal, with a tidal amplitude of 1.1–1.5 m. The estuarine site is a low salinity system with significant freshwater input, particularly during the summer time.

In recent years, the smooth cordgrass Spartina alterniflora, native to North America, is invading to the mudflats and habitat of native saltmarsh vegetation (Suaeda Salsa) has been increasingly common at the seaward edge, in the Yellow River Delta (Yan et al. 2020). The cordgrass now at its early stage of invasion has a mean stem height of 1.16 ± 0.08 m, a shoot density of 528 stems/m2 and the mean shoot diameter at the base was 0.058 ± 0.021 m. While invasive S. alterniflora has replaced native plant communities, and large-area of new wetlands are forming at the forepart due to the high sedimentation. Nevertheless, in recent years, some areas experienced extensive erosion resulting in rapid habitat loss and fragmentation of the cordgrass habitat that suffered from erosion induced by hydrodynamics, with a conspicuous pattern of patchiness (See Plate 1A and B).

Resource retention is an important component of landscape function in such a fragmented habitats, with patches serving as sink zones, capturing water-flow, sediments and nutrients from inter-patches or source areas. In the Yellow River Delta, a large area of seaward tidal flats are covered shell debris, mainly constituted of empty bivalve shells,
such as mussels, oysters, clams and scallops, forming coexistent pattern of shell aggregation behind the isolated patches (See Plate 1C and D). Shells are present on surface sediments and are also vertically distributed in a relatively thick layer (ca. 10–15 cm) depending on the sites and patch sizes. Shell aggregation prolonged the patch length/width, lowering the steep slope around the patch and forming a stable substrate in contrast to the highly unstable seaward substrate without shell aggregation. This spatial configuration provides an exceptional opportunity to test how these remnant patches, shell debris and plant density interact to control the persistence of tidal systems in face of sea level rise and human impacts (Plate 2).

2.2. Field surveys

To investigate the potential impacts of patch size of *S. alterniflora*, prior to setting up our sampling plan, we first identified the patch size of cordgrass which distributed on the mudflats. The number of remnant patch was counted and it was investigated whether the size-frequency relationship could be an indication for field surveys with detailed measurements. We quantified the area of each patch along three intertidal line transects running from high to low intertidal perpendicular to the water line. Replicate transects were separated by at least 30 m, and each at least across 100 m width. All measurement of patch sizes was performed during minimum above-ground biomass presence, during the time of ramets of parental plant, in early Spring 2018. In the field, although individual patches have irregular shapes, they were standardized as circular, so the cover area of each vegetation patch can be quickly calculated. After the measurement of patch sizes, all the patches were divided into several groups by every 5 m² of constant area to know the distribution frequency of different patch sizes. We observed the abundant patches with an average area of 20–40 m² (Fig. 1).

To examine the interactive effects of patch size, plant density and shell aggregation on the patch stability and resilience of plant community at patch-level. We investigated the relationships between shell aggregation and stem density inner- and on the edge of the vegetation patch and patch size, to visualize whether shell aggregation and stem
density varying with position depends on the patch size. To obtain empirical data of both stem density and shell aggregation, we encompassed a wider range of patch size. Therefore, eleven patches differed with patch size were selected, which were parallel to the water line to create a relative homogenized transect with similar tidal levels. The patch size treatments varying with sizes were located >20 m from one of the two lateral edges of a given \textit{S. alterniflora} patch. This distance was chosen to avoid any “edge effects” (i.e., waves wrapping around the ends of patch) and was based on lateral flow velocity profiles behind patches.

To know whether plant density can feedback to increase sediment accretion and maintain a stable patch, we established the relationships between patch height, average patch height, scouring width around the patch and patch size (See the research diagram of Plate 2). The patch height, cliff height, scouring width, weight and length of shell aggregation patch on the edge of patch, as well as the stem density inner patch and on the edge of patches were evaluated manually. We sieved and weighed the shell debris by digging a 20 × 20 × 20 cm plot. We quantified per cent coverage of shells within a 1.0 m² plot by dividing them into one hundred 10 × 10 cm quadrats inner each patch. Patch height and cliff height of each patch were calculated relative to the ground surrounding the \textit{S. alterniflora} patch (See Plate 2 depicting the height, cliff height and the scoring density). Patch height within each patch was measured for a potential indication of patch size-dependent effect on sedimentation within patch, accounting for the local positive feedback between plant-density and sediment accretion (Bouma et al. 2009). For scouring process around patches, the width of deep area around the patch was quantified by measuring the maximum distance from the ridge of scouring area to the cliff of the patch (See Plate 2). The final scouring intensity by quantifying the width of scouring area was related to the total patch size as it was assumed that different patches cause the varied magnitude of the negative feedback. We use both linear and non-linear regression analysis to detect the relationships between patch size and stem density, patch height, cliff height, scouring width, prolonged length of shell aggregation, shell coverage within patch and shell density on the edge patch, as well as coverage of shells within patch, density of shells on the edge of patches and stem density inner and on the edge of the patches.

2.3. Manipulative experiments

To test the shell aggregation impacts on plant community persistence depending on patch size, manipulative experiments were performed by removing the shell debris within and on the edge of the patches. In April 2018, we selected 10 patches that were parallel to the water line to create a relative homogenized transect with similar tidal levels. Five small patches with an average area of ~18 m² and five big patches with an average area of ~34 m² were assigned as two patch-size differed groups. At each patch location, two treatments with and without shell removal were assigned to examine the shell aggregation impacts within the central patch and on the edge of the patch. First, to test the shell aggregation impacts on the regrowth of the plant within the patch, 4 quadrats (1 × 1 m²) were positioned in the core center of the patches, then we removed two of the four quadrats in diagonal line. Secondly, to examine the shell aggregation impacts on the regrowth of plants on the edge of the patch, we only removed the shells around the plants with two 1 × 1 m² quadrat at the landward direction (ebbing direction) and two marked unmanipulative quadrats. Shells removal of the two quadrats was performed during low tide and designed as the manipulative treatments and the other two quadrats without removal designed as the control. Before shells removal, we quantified each quadrats to get the net changes of ramet density after shells removal between the removal and control. To test the effects of shell
aggregation on the cordgrass re-growth within the patch and on the edge of the patch, we compared the density changes with shells removal and control (unmanipulation) to the density before removal. Then we calculated the net changes in density of *S. alterniflora* between removal and unmanipulation of both the small and big patch size groups.

To detect shell removal impacts on patch stability, after 3 weeks’ experiment of shell removal within the central and on edge of each patch, we conducted a destructive experiment to remove all the prolonged section that covered by shell debris. We quantified the absolute retreat distance of each patch to its original patch border (identified with plant growing on the edge) before removal to see its influences on patch contraction or patch stability. After 3 weeks, the net retreat distance of patch edge/border was determined by measuring the linear distance between its original and final location. At the end of the experiment, the ratio of net retreat distance to each patch area was calculated as a function to determine the net effect of shells removal on the patch stability between big and small patch-size groups. We compared net increase of stem density with shells removal, within and on the edge of patch between the big and small patch size groups, with a two-way ANOVA and Tukey’s HSD comparisons. Analyses were conducted using R 3.4.1 (Team 2017).

3. Results

3.1. Relationship between patch size and patch morphology

Average height of the central patch was defined to indicate the difference between patch elevation within the central patch and edge cliff height. Our results showed that patch height measured within vegetated zones (33.2 cm) was significantly higher than the cliff height that adjacent non-vegetated zones (19.7 cm) (Two-tailed t-test, *n* = 64, *F* = 5.08, *P* = 0.028). The significant difference was strongly attributed to the scouring intensity, explaining the heavy erosion process around the patch. This indicates significant linkage between vegetation presence and increased sedimentation within the patch, and increased erosion around the patch. Importantly, patch height (Fig. 2A), cliff height of the patch (Fig. 2B) and width of scouring area around patch increased linearly with increasing patch size (Fig. 2C), showing a patch size-dependent positive feedbacks.

3.2. Relationship between patch size and plant density

Positive relationships between patch size and stem density were non-linear for both the central patch (Fig. 3A) and on the edge of the patch (Fig. 3B). In general, stem density of the inner central patch (86.0 ind/m²) was a little bit lower than that on the edge of the patch with shell aggregation along the patch (93.4 ind/m²), but it was not significant (Two-tailed t-test, *n* = 64, *F* = 2.08, *P* = 0.153). This suggests shell aggregation/presence appears can be beneficial to the growth of plant there, therefore weakening the negative effect of hydrodynamic forcing on plant growth.

3.3. Relationship between patch size and shells aggregation

Shell aggregation was significantly related to patch size. Length of shell aggregation (landward border of aggregation to patch edge)
behind the patch increased non-linearly with increasing patch size (Fig. 4A). Weight of shell aggregation on the edge of the patch increased linearly with increasing patch size (Fig. 4B). In contrast, the coverage of shells within the central patch was detected with significant non-linear relationship in quadratic term, suggesting both small and big patch can trap less shells within the patches (Fig. 4C). Our statistical analysis indicates a threshold of patch size ~20 m² covered the largest number of shells (Fig. 4C), explaining a state transition of shell aggregation and magnitude.

3.4. Relationship between shell aggregation and plant density

Stem density in the central patch and on the edge of patch, were both positively linked to weight of shells along the patch edge in linear terms (Fig. 5A and B). We also detected that stem density decreased linearly with increasing of shells coverage within the patch (Fig. 5C), while we did not find any significant relationship between stem density on the patch edge and shells coverage in the patch (Fig. 5D). Therefore, our results suggest that shell aggregation inner patch would impair the growth of plant, while shell aggregation on the edge can facilitate the plant growth.

3.5. Interaction of shell debris and patch size on plant re-growth and patch stability

Computation of net increase of plant re-growth emphasized that shell aggregation is also an important factor determining the ability of remnant patch size to maintain the community persistence on the edge of the patch. Our results showed that shells removal (F1, 20 = 33.15, P < 0.001, Fig. 6A) and patch size (F1, 20 = 81.32, P < 0.001, Fig. 6A) significantly affected the plant growth inner the patch, and we observed a significant interaction between the two main factors (F1, 20 = 10.57, P = 0.005, Fig. 6A), indicating that shell aggregation strongly affect the ability of remnant fragmented patch to facilitate plant persistence inner central patch. In addition, our results showed that shells removal (F1, 20 = 60.00, P < 0.001, Fig. 6B) and patch size (F1, 20 = 23.27, P < 0.001, Fig. 6B) significantly influenced the regrowth of vegetation on the patch edge, but also with significant interaction between the two main factors (F1, 20 = 29.91, P < 0.001, Fig. 6B). Therefore, our results suggest that shells removal within central patch amplified the positive effect of patch size on plant growth, but shells removal on the edge of the patch inhibited the plant re-growth.

Removal of all the shells aggregated behind the remnant patches showed that the retreat distance per unit patch area differed significantly depending on the patch size group. The ratio of retreat distance to patch size was significant larger of the bigger patch group than the smaller (F1, 10 = 10.28, P = 0.013, Fig. 7). This suggests that big patch with shell aggregation along the patch can further facilitate the patch stability through decreasing erosion.

4. Discussion

Given continued biodiversity declines, and increasing coastal vegetated degradation globally, the status of remaining habitat fragments is becoming increasingly important. Despite increasing evidence shows that the patchiness of habitat fragmentation often controls ecosystem stability and resilience (Haddad et al. 2015), the mechanisms underlying patch-level persistence to physical stress remain poorly understood. Here, we report both survey and experiment evidence that feedback mechanisms involve interactions among the habitat-forming plant density, patch size and associated shell aggregation determining the persistence of a degrading salt marsh. Our findings reveal positive interactions between patch size of remnants, plant density and multitude of shell aggregation along patch edge rather than patch interior. Large patches harboring more plants can trap more shell debris along the patches, thus protecting the patch edge from erosion. By contrast, small patches trap lesser shell debris along the patches but are able to accumulate more shells within the patches, therefore inhibiting the re-growth of the plants. This critical state shift of shell aggregation depends on patch size, indicating a critical threshold of patch size ~20 m² below which ecosystem collapses. Our findings demonstrate that, depending on the self-reinforcing feedbacks involved, the capacity of a degrading ecosystem to mitigate environmental stress is typically both density- and patch size-dependent. Our study also adds the evidence that shell formation by mollusks is an important ecosystem engineering process to inform transition states of degradation-prone ecosystem by controlling the dynamic of stress-resistant patches.

General consideration of detrimental effects of patchiness deriving from fragmentation has been widely documented at landscape scales (Fahrig 2003; Fischer and Lindenmayer 2007). Whether systems dominated by strong or weak interactions are resilient is still contentious, proposing the focus on the role of organism–environment feedbacks in the context of habitat patchiness (Thrush et al. 2009; Zee and Fukami 2015). Increasing evidence shows that habitat fragmentation is, in particular, harmful to habitat-forming species, such as salt marsh plant, seagrass.

![Image](https://example.com/image.png)

Fig. 4. Vegetation patch size impacts on the shell aggregation at different positions of the patch. Relationships between vegetation patch size and length of patches shell aggregation (A) (i.e. the distance to the vegetation patch landward), weight of the shells on the edge of the vegetation patch (B) and the coverage of shells inner the patch (C) in a fragmented Spartina alterniflora undergone heavy erosion events in the Yellow River Estuary.

![Graph](https://example.com/graph.png)
and macroalgae, and the ability to modify habitats favoring a resistant and persistent community to massive environment disturbance is often related to self-reinforcing feedback processes (Angelini et al. 2016). Our study clearly highlights the habitat patchiness of fragmentation of a degrading saltmarsh ecosystem is more persistent, through positive interactions between plant densities, patch size and shell aggregation. Moreover, all three processes are interrelated; therefore, changes in one of these processes can potentially have cascading effects on the other processes. Therefore, our results demonstrate that complex positive interactions can strengthen saltmarsh plant persistence following habitat fragmentation in patchiness, the capacity depends on the degree of patchiness in fragments, and how they are affected by other human-induced environmental stressors (e.g. shell formation and production).

Vulnerability of a particular plant community to multiple-physical stresses at the patch level, may be shaped by patch size dependent biological and physical processes. More currently, conservation planning principles of representativeness and complementarity have widely focused on large intact landscapes, with emphasizing the importance of large, connected patches of habitat for ensuring the persistence of species and conserving species richness, in contrast to vulnerability of fragmented landscapes comprising many small, isolated patches with extensive edge environments (Murcia 1995; Foreman 1996; Wintle 2018). Our findings reveal that habitat fragmentation resulting in the form of small and isolated patches can still persist, considering the positive feedback between vegetation and sedimentation (i.e. shell debris) allows the vegetation patches to gain sediment stability and elevation and would therefore increase flow resistance (Temmerman et al. 2007; Bouma et al. 2009; Schwarz et al. 2014; D’Alpaos et al. 2017). Our study provides evidence that small and isolated patches of remnant habitats in fragmented landscapes tend to persist by harboring unique positive interactions between plant and physical forces that are not well represented in large intact landscapes. Therefore, we argue that the robustness of saltmarsh habitats to stochastic perturbations in a...
patchiness landscape, tends to be underestimated without considering positive biophysical feedback processes knowing to enhance plant persistence and patch stability through patch size-dependent associative processes.

Increasing evidence suggests that multiple feedbacks are likely to act simultaneously and that their combined effects or interactions may affect ecosystem responses to environmental change, but the vast majority of studies have focused on individual feedbacks (Funk et al. 2017; Maxwell et al. 2017). Our study provides empirical results in a fragmented coastal saltmarsh ecosystem, self-reinforcing feedbacks are identified to be a threshold response to patch sizes, with plants growth remaining stable in large patch sizes, then dropping rapidly below a patch size of ~20 m². Large patches with more plants enhance their persistence by capturing more shells at the edge of the patch, which can reduce erosion induced by hydrodynamics. However, small patches with fewer plants cannot persist, because shells are trapped mainly inside of the patch rather than the edge, which hinders plant regeneration in the following growing season. This finding suggests that the relative importance of shell aggregation in governing the resilience of saltmarsh plants will vary depending on patch size that determines where the engineering processes take place. Therefore, our study highlights that habitat patchiness associated with feedbacks are likely to be strongly site-specific, scale-dependent, the morphological traits of dominant habitat-forming species and the gradients of environmental conditions. Our study provides valuable insights into the self-reinforcing feedbacks underlie system dynamics and ecological resilience.

Knowing persistence of habitat patchiness of fragmentation requires determining whether there are thresholds that separate different ecological processes and interactions in governing stability. Although habitat patchiness of fragmentation has the capacity to maintain functioning, structure, and feedbacks in the face of both internal and external drivers (Folke et al. 2004; Cumming et al. 2005), the outcomes can be persistent and deleterious, but often unpredicted. A recent study demonstrates that stress-resistant saltmarsh plant patches can have a disproportionately large effect on ecosystem recovery by virtue of the fundamental spatial processes they support, indicating the importance of remnant patches acting as habitat growth nuclei controls ecosystem persistence (Cumming 2016). Our study suggests that despite disturbances being nearly continuous in nature, communities do not constantly shift from degrading state to collapse, but can persist by the interaction of patch properties and external shell production. Position and magnitude of shell aggregation varying with patch size, the spatial thresholds (e.g. determining shells on patch edge or center) could provide useful insight into processes and interactions around thresholds of patch size. Our results indicate that the decline in coverage of shell inner patches is highly non-linear, with a well-defined threshold below ~20 m² which patch collapses. Therefore, our findings emphasize the importance of shell formation by mollusks subjects to human exploitation and climatic changes that is an important ecosystem engineering process controlling the dynamic of stress-resistant patches.

Predicting how habitat fragmentation interacts with other stressors that threaten species of conservation is an important challenge for ecosystem-based management. We provide strong evidence of self-reinforcing feedbacks of habitat-forming plants to strengthen ecosystem persistence, in particular, the under-appreciated importance of patch size-dependent shell aggregation can be important engineering process in attenuating hydrodynamics. Our findings enrich the theory that despite resilience is often implicit concept that refers to broad-scale changes (Dayton et al. 1984), it can also apply at the local patch scale, with implying that habitat patchiness deriving from fragmentation was able to be generated by positive interactions among internal and external forces in patch-level.

Our study cautions that management practices that obscure, remove, or ignore stabilizing feedbacks that underlie the provision of desired ecosystem services can erode the persistence and resilience of a degrading ecosystem. To ensure persistence of habitat-forming species in the face of both climate changes and human-modification of the landscapes, a combination of major resources reutilization, for instance shell debris of bivalves, along with significant reductions in habitat fragmentation are required. These insights will be increasingly critical for managing and prioritizing areas of preservation and ecological restoration in fragmented landscapes.

**CRediT authorship contribution statement**

J.Y., T.v.d.H. and B.C designed the research; J.Y and H.C·S led to perform the field experiments and lab analysis; J.Y., T.v.d.H. conceived the writing with contributions from all authors; all authors contributed substantially to manuscript direction and revisions.

**Declaration of competing interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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**Fig. 7.** Mean (±se) absolute retreat distance to unit patch size (i.e. ratio = retreat distance to the original edge/patch size), with removing all the aggregated shells behind the vegetation patches, as a function to standardize the patch effect. Different letters above means indicate a significant mean comparison.


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