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REVIEW

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Facilitating foundation species: The potential for plant–bivalve interactions to improve habitat restoration success

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Abstract

1. Vegetated marine and freshwater habitats are being increasingly lost around the world. Habitat restoration is a critical step for conserving these valuable habitats, but new approaches are needed to increase restoration success and ensure their survival.
2. We investigated interactions between plants and bivalves through a review and analysis of 491 studies, determined the effects, mechanisms and key environmental variables involved in and driving positive and negative interactions, and produced guidelines for integrating positive interactions into restoration efforts in different habitats.
3. Fifty per cent of all interactions (both correlative and experimental studies) were positive. These were predominant between epifaunal bivalves and plants in all habitats, and between infaunal bivalves and plants in subtidal habitats. Plants primarily promoted bivalve survival and abundance by providing substrate and shelter, while bivalves promoted plant growth and survival by stabilizing and fertilizing the sediment, and reducing water turbidity. The prevalence of positive interactions increased with water temperature in subtidal habitats, but decreased with water temperature in intertidal habitats. The subset of studies conducted in a restoration context also showed mostly positive interactions.

4. Twenty-five per cent of all interactions were negative, and these were predominant between plants and infaunal bivalves in intertidal habitats, except sulphide-metabolizing bivalves, which facilitated plant survival. Interactions involving non-native species were also mostly negative.
5. *Synthesis and applications*. Promoting facilitative interactions through plant–bivalve co-restoration can increase restoration success. The prevalence of positive interactions depends on habitat and environmental conditions such as temperature, and was especially important in subtidal habitats (involving both infaunal and epifaunal bivalves) and in intertidal habitats (involving only epifaunal bivalves). Thus sites and species for co-restoration must be carefully chosen to maximize the chances of success. If done properly, co-restoration could increase initial survival, persistence and resilience of foundation species, and promote the recovery of associated biodiversity and ecosystem services.

KEYWORDS
bivalves, co-restoration, ecosystem engineers, facilitation, habitat restoration, plant–bivalve interactions, salt marsh, seagrass

1 | INTRODUCTION

Marine and freshwater vegetated ecosystems are being lost at unprecedented rates due to anthropogenic impacts (Lotze et al., 2006; Zhang et al., 2017). These losses have led to declining ecosystem services such as biodiversity provisioning, coastal protection and carbon sequestration (Barbier et al., 2011). While policies have been enacted to protect ecosystems from further degradation, many cannot recover without human intervention, i.e. restoration (Jones et al., 2018). However, restoration success rates can be low in marine habitats (e.g. seagrass meadows: 38%; Bayraktarov et al., 2016), and new approaches are needed to enhance the initial establishment success of foundation species and ensure the long-term persistence of restored habitats.

Recent studies have shown that promoting positive interactions between individuals of the same species can increase restoration success (de Paoli et al., 2017; Silliman et al., 2015; van der Heide et al., 2007), highlighting the importance of facilitative interactions in restoring ecosystem-engineering species (Maxwell et al., 2017). Facilitative interactions between ecosystem engineers may be equally important for promoting resilience and recovery (Angelini et al., 2016; Derksen-Hoojiberg et al., 2018; Renzi, He, & Silliman, 2019; van de Koppel et al., 2015), but <3% of restoration projects have integrated interspecific interactions (Zhang et al., 2018).

Here, we considered interactions between two widespread groups of ecosystem engineers that commonly co-occur in marine and freshwater habitats: plants and bivalves. As both positive and negative interactions have been reported, incorporating them into restoration efforts requires understanding the factors that determine the outcome of the interaction. Environmental stressors can cause shifts from facilitation to competition, or vice versa (Crain & Bertness, 2006). Positive interactions may be especially important in stressful environmental conditions (Bertness & Callaway, 1994), and could thus be more common in intertidal (high-stress hydrodynamics conditions with high variations in light and temperature; Tomanek & Helmuth, 2002) than subtidal (lower-stress hydrodynamics and stable conditions) habitats. Exposure to stressors such as temperature, light, ice cover and desiccation also varies between infaunal (below-ground) and epifaunal (above-ground) bivalves, and along latitude (e.g. McAfee, Cole, & Bishop, 2016).

Here, we investigated plant–bivalve interactions in marine and freshwater habitats through a review and analysis of 491 studies. We aimed to (a) identify the effects and mechanisms involved in these interactions, (b) understand which environmental conditions and variables affect the predominance of positive and negative interactions and (c) outline guidelines for plant–bivalve co-restoration in different habitats with the aim of increasing restoration success and the recovery of associated biodiversity and ecosystem services.

2 | MATERIALS AND METHODS

2.1 | Literature search and categorization

We performed a search (see Appendix S1) on Web of Science and Google Scholar using the Boolean search terms: '(seagrass* OR plant* OR vegetation OR *grass* OR *weed* OR angiosperm*) AND (bivalve* OR clam* OR cockle* OR mussel* OR oyster* OR quahog* OR scallop* OR *shell*)'. We separated individual studies based on study type (correlative vs. experimental), and/or method (field vs. laboratory/mesocosm). Studies on different species in the same manuscript were also separated, unless focused on a species assemblage.

We extracted data on the environmental variables, species, effects and mechanisms (Table S1). We categorized each study as either correlative (field surveys that could not show causation), or experimental (manipulative experiments, in two subcategories: plant effects on bivalves, and bivalve effects on plants), and then by habitat (freshwater submerged aquatic vegetation [SAV], mangrove, salt marsh, intertidal seagrass, subtidal seagrass) and bivalve type (infaunal, epifaunal). We extracted geographic information (latitude, ocean basin, hemisphere), spatial and temporal scales, whether the study involved within-habitat (plants and bivalves co-occurring in the same habitat) or cross-habitat (plants and bivalves adjacent or apart in the same area) interactions, species, whether they were native or non-native and the variables measured.

Temperature is an important stressor for ecosystem engineers (Collier & Waycott, 2014), and is likely to become increasingly so due to climate change. We thus determined the mean summer surface temperature (MSST) and mean winter surface temperature (MWST) for each study. For marine and North American Great Lakes studies, we calculated MSST for June–July (Northern Hemisphere) or January–February (Southern Hemisphere) and MSWT for the opposite months from a 6-year daily mean (2010–2015) from the Met Office Hadley Centre (Rayner, 2003; hadobs.metoffice.com/hadisst/). For other freshwater studies, MSST and MSWT were calculated for July–September and January–March based on a 5-year (2005–2009) monthly mean from Sharma et al. (2014, 2015).

In order to include all studies in the statistical analysis, which involved vastly different approaches, treatments and responding variables, we used a vote-counting approach by assigning an overall effect (positive, negative, mixed, non-significant), to each study. This overall effect was based on the statistically significant results presented in each study (Table 1). We also noted the positive and negative mechanisms involved in the effect.

TABLE 1 Description of the overall effects extracted from the 491 studies

Overall effect	Description
Positive	The study includes only statistically significant positive results. It may also include non-significant results
Mixed	The study includes both statistically significant positive and negative results. It may also include non-significant results
Negative	The study includes only statistically significant negative results. It may also include non-significant results
Non-significant	The study includes no statistically significant results

2.2 | Statistical analyses

We first used two-proportion *Z*-tests to determine whether the proportion of positive effects differed between studies involving native versus non-native species. As they differed significantly, we proceeded with all following analyses using only studies of native species ($n = 409$). We ran two-proportion *Z*-tests to determine whether the proportion of positive effects differed between: cross- versus within-habitat, restoration versus non-restoration studies, study types (correlative vs. experimental, plant effects on bivalves vs. bivalve effects on plants) and temporal scales (correlative: single vs. multiple sampling, experimental: single year vs. multi-year experiments).

We used cumulative link models (CLMs; Agresti, 2013) to determine which variables (Latitude, Habitat, Tidal zone, Bivalve group, MSST, MWST, Spatial scale; Table S1), contributed to the overall effect. CLMs are comparable to Generalized Linear Models, but use ordered categorical response variables (the overall effect ordered as: negative, mixed, positive, excluding non-significant studies) with no assumption of the distance between classes. We excluded studies on non-native species, those without temperature data and those including multiple bivalve groups and tidal zones ($n = 360$). We used the CLM function (package ORDINAL; Christensen, 2018), in R version 3.51 to create a set of candidate models which included all combinations of predictor variables (using MuMIn package; Bartoń, 2018), excluding models with correlated variables (Latitude-MSST-MWST and Habitat-Tidal zone), ordered according to the Bayesian information criterion (BIC). From a subset of the best models (delta BIC < 4), we calculated the most important predictor variables.

3 | RESULTS

3.1 | Habitats, species and variables

Overall, we examined 491 studies from 225 publications (see Data sources for list of included in the review): 246 correlative and 245 experimental (Figure S1; Table Agresti,S2). Subtidal seagrasses accounted for 50% of the studies, followed by salt marshes (15%), intertidal seagrasses (14%), freshwater SAV (11%) and mangroves (9%). Eighty-two plant taxa were studied (32 freshwater macrophytes, 28 seagrasses, 14 salt marsh plants and 8 mangroves; Table S3), and eelgrass *Zostera marina* accounted for ~40% of the studies (Figure S2). Among the 136 bivalve taxa studied (40 epifaunal, 96 infaunal; Table S4), *Mytilus edulis*, *Geukensia demissa* and *Mercenaria mercenaria* were the most studied (Figure S3). About 92% of studies (452) involved within-habitat interactions, and 18% of experimental studies (44) were conducted in a restoration context (Table S4).

The geographic distribution of studies likely reflected differences in research effort: 86% of studies were in the Northern Hemisphere, and only 14% in the Southern Hemisphere (Figure 1; Tables S5 and S6). Most marine studies took place in the Atlantic

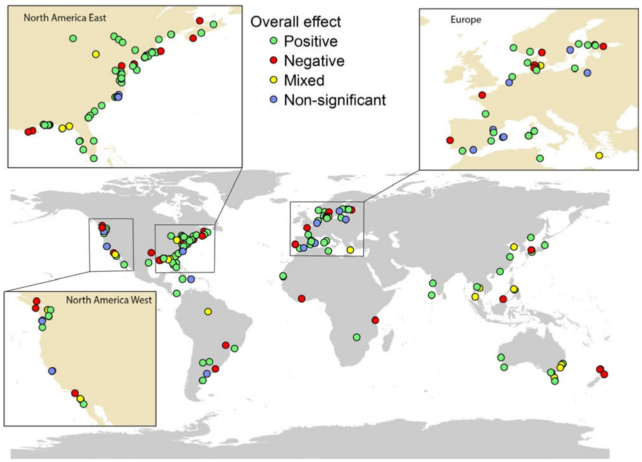

FIGURE 1 Geographic distribution of studies by overall effect. See Tables S6 and S7 for geographic distribution by study type and habitat

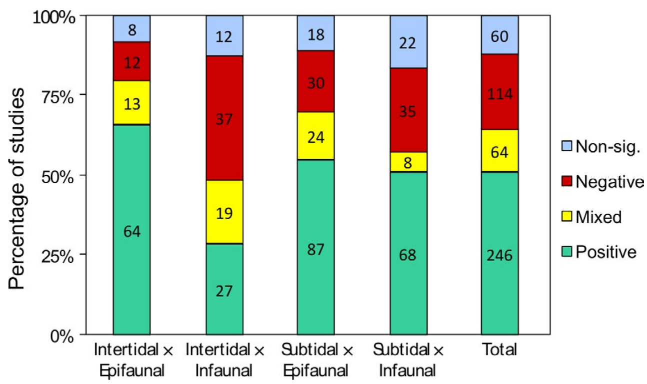

FIGURE 2 Overall effects of plant–bivalve interactions by habitat and bivalve type (n = 491). Seven studies included multiple habitat or bivalve types. See Figure S6 for effects by study type in different habitats

Ocean (66%), followed by the Pacific Ocean (27%), while most freshwater studies were in North America (46%) and Europe (27%; Table S5). Most studies were conducted in the field at spatial scales of 1–100 km (Figure S4a), and involved a single sampling event (correlative), or an experiment lasting a single season or year (Figure S4b). Common variables included plant and bivalve abundance, growth and reproduction, as well as water turbidity, nutrients and sulphides (Table S8).

3.2 | Interactions and effects

Overall, positive interactions were reported in 51% of studies, and negative interactions in 24% (Figure 2). Interactions between epifaunal bivalves and plants were mostly positive in both intertidal and subtidal habitats, and between infaunal bivalves and plants in subtidal habitats, whereas interactions between infaunal bivalves and plants in intertidal habitats were mostly negative (Figure 2). There were no differences between study types, nor between

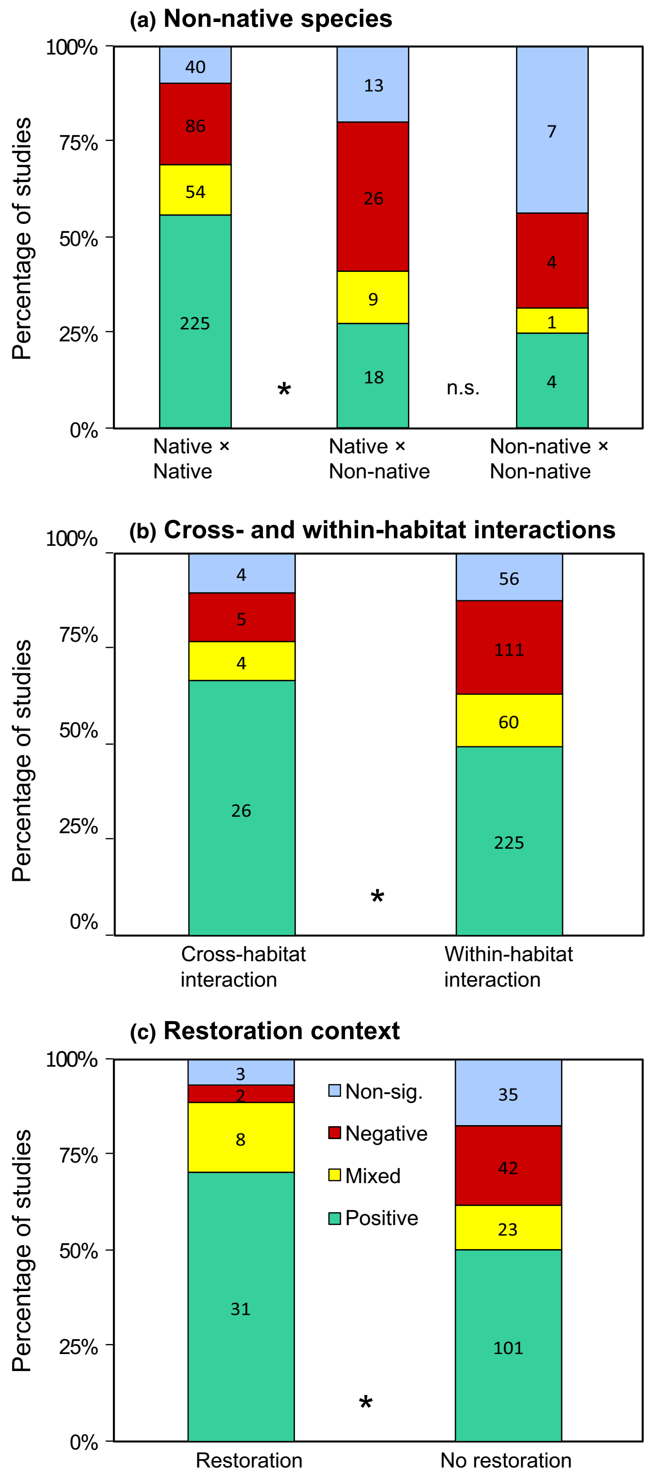

FIGURE 3 Differences in overall effects between (a) native and non-native species, (b) cross- and within-habitat interactions and (c) studies in a restoration context. An asterisk indicates a significant difference in the proportion of positive interactions

temporal scales. There were significantly higher proportions of positive interactions in studies of native species than those including at least one non-native species (Figure 3; Table S9), and significantly higher proportions of positive interactions in cross- than within-habitat studies and in restoration than non-restoration studies

(Figure S4; Table S9). In particular, all co-restoration studies showed positive interactions (Table S5).

The CLM analysis showed that the three most important factors explaining the overall effect were bivalve group, tidal zone and MSST

TABLE 2 The relative importance of variables in determining plant–bivalve interactions, calculated from a subset of the best models (delta Bayesian information criterion [BIC] < 4; Table S10) in the cumulative link modelling analysis

Variable	Relative importance (proportion of models in which variable is included)
Bivalve group	1
Tidal zone	0.60
Bivalve group × Tidal zone	0.35
MSST	0.31
Spatial scale	0.29
MSST × Tidal zone	0.26
MWST	0.24
MWST × Tidal zone	0.24

Abbreviations: MSST, mean summer surface temperature; MWST, mean winter surface temperature.

(Table 2). We thus chose a model including these factors (Model 3; Table S10) to calculate the probability of positive, negative and mixed interactions across a temperature gradient. We found that the proportion of positive interactions increased with MSST in subtidal habitats, and became predominantly positive at ~10 and ~16°C for epifaunal and infaunal bivalves respectively (Figure 4). However, in intertidal habitats, the proportion of negative interactions increased with MSST. For epifaunal bivalves, positive interactions were still predominant across all temperatures, but for infaunal bivalves, negative interactions became more dominant at ~23°C (Figure 4). We repeated this analysis using a model including MSWT instead of MSST (Model 2) and found the same interaction of temperature with bivalve group and tidal zone. There were no differences in overall effect according to the type of study (Figure S5).

3.3 | Mechanisms

About 64% of experimental studies identified mechanisms (20% did not, while the remaining 16% found no significant effects). The most important mechanisms mostly differed by tidal zone and bivalve type (Figures 5 and 6; Tables 3 and 4). A detailed overlook of the most important positive and negative mechanisms and effects in

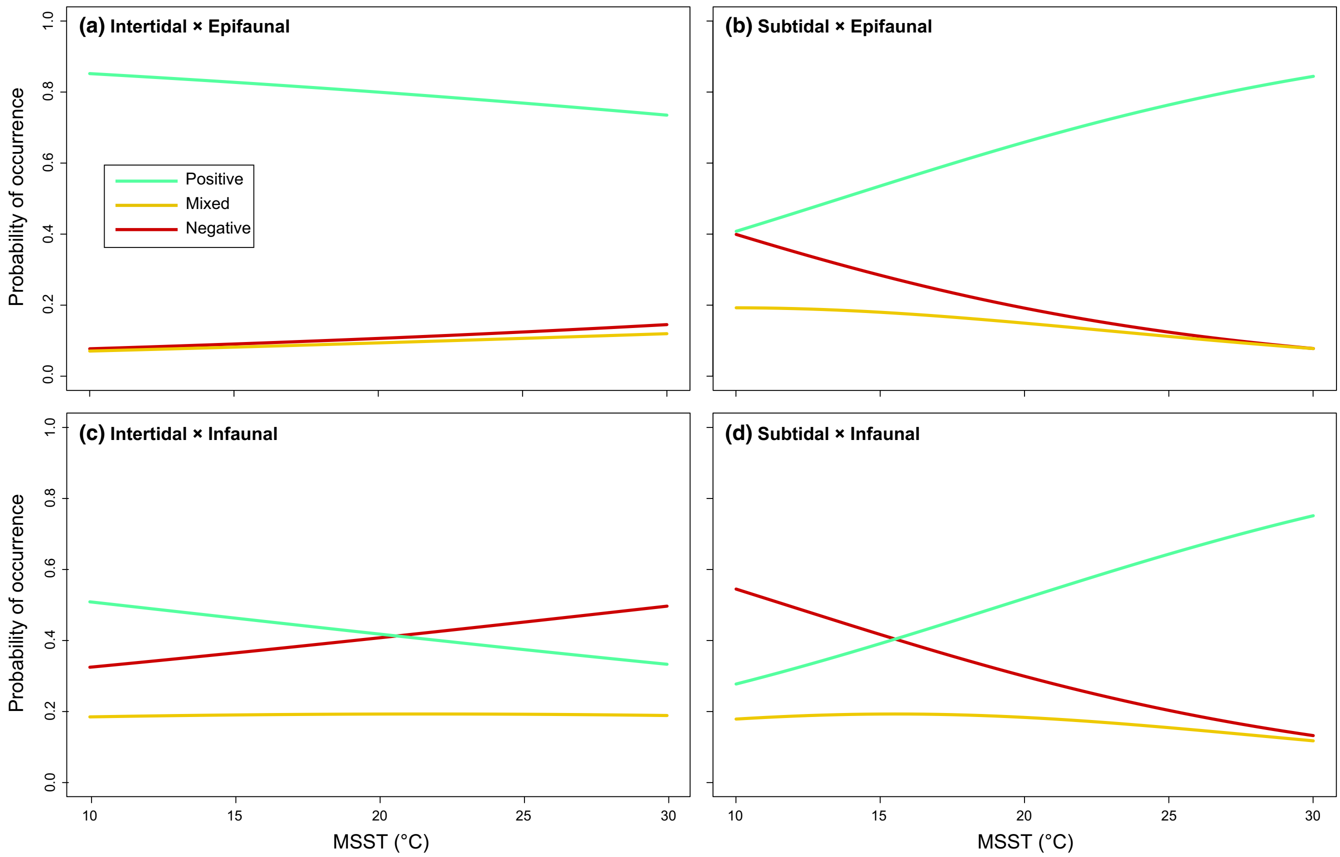

FIGURE 4 Effects of mean summer surface temperature (MSST) on the probability of positive, mixed, and negative interactions between plants and epifaunal (a,b) and infaunal (c,d) bivalves in intertidal (a,c) and subtidal (b,d) habitats

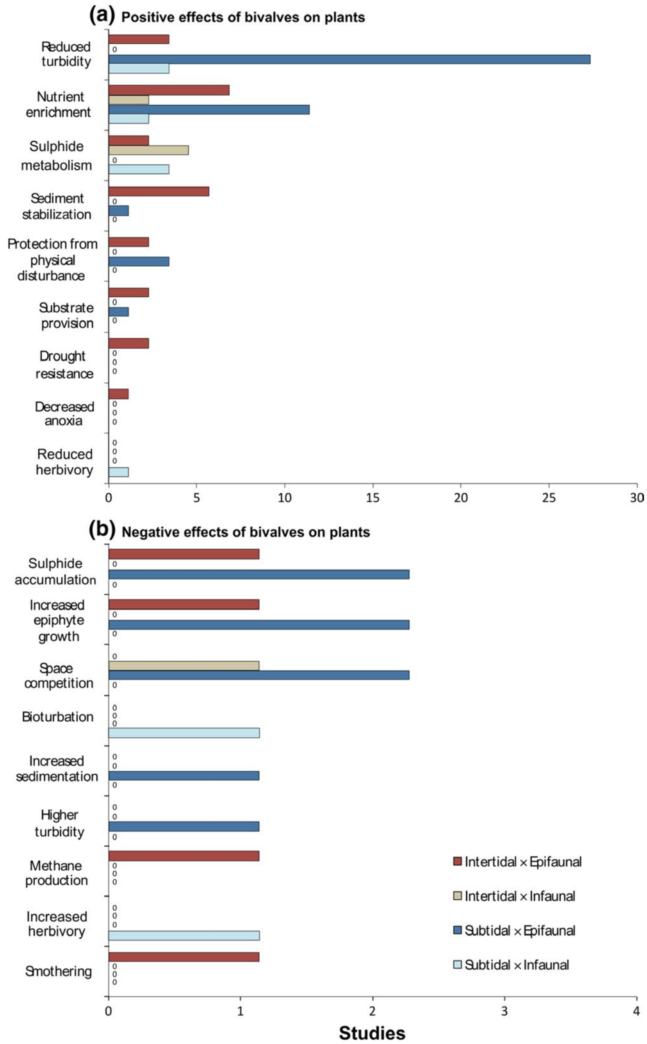

FIGURE 5 (a) Positive and (b) negative mechanisms by which bivalves affect plants. Each mechanism can lead to several effects (Table 3)

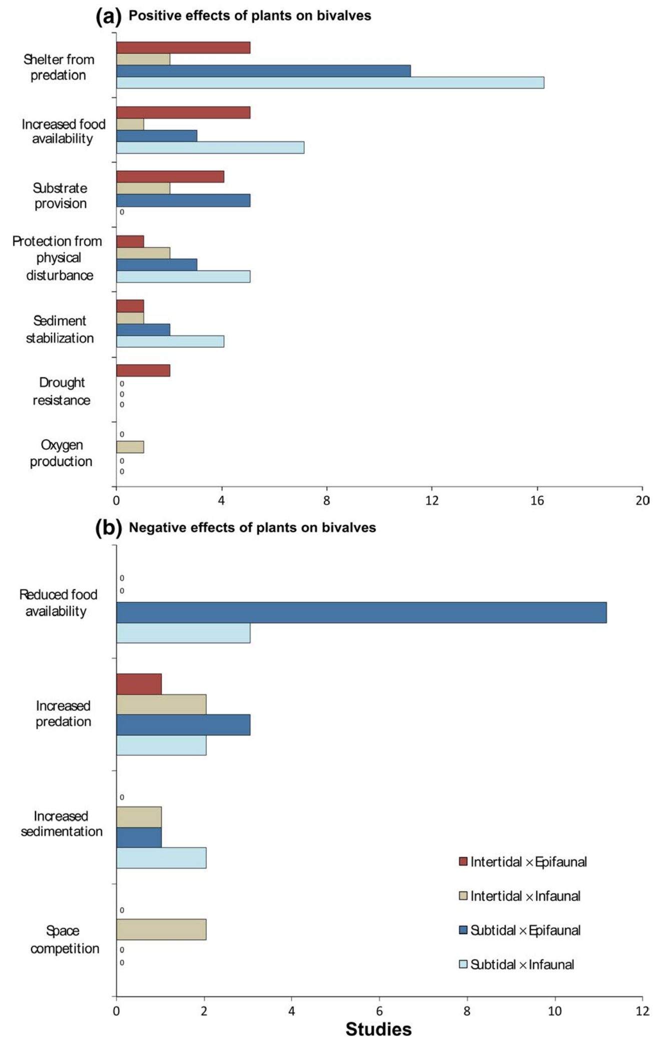

FIGURE 6 (a) Positive and (b) negative mechanisms by which plants can affect bivalves. Each mechanism can lead to several effects (Table 4)

each habitat, as well as their implications for restoration, are presented in the discussion below.

4 | DISCUSSION

Through a global literature review, we highlight the importance of plant–bivalve interactions and clarify the most important environmental variables driving these interactions. The relative prevalence of positive versus negative interactions depended on the bivalve type, tidal zone and water temperature. Interactions between epifaunal bivalves and plants were predominantly positive in all habitats, while interactions between infaunal bivalves and plants differed by habitat—positive in subtidal habitats, but negative in intertidal habitats. Statistical modelling showed that water temperature played an important role in regulating these interactions. Positive interactions became more prevalent as water temperatures increased in subtidal habitats, possibly due to increased facilitation in response to stress (Bertness & Callaway, 1994). However, negative interactions became more prevalent with higher water temperatures in intertidal habitats—possibly because space competition seems to be an important aspect in the intertidal zone that has increasingly serious consequences as temperature increases (e.g. increased desiccation risk). Positive interactions were especially prevalent in co-restoration studies, supporting increased integration of plant–bivalve interactions into restoration efforts.

Below, we review and discuss prevailing plant–bivalve interactions and mechanisms in each habitat, then discuss general implications for restoration as well as aspects in need of additional research effort. We also note that our vote-counting approach, which was chosen in order to incorporate very different types of studies into the same analysis, does have drawbacks. Most notably, we cannot discuss or predict the effect sizes of these different mechanisms by which plants affect bivalves or bivalves affect plants. Finally, we outline a framework for determining effective co-restoration strategies depending on the focal habitat and species, as well as the local environmental conditions.

TABLE 3 Positive (+) and negative (−) effects of bivalves on plants (see Figure 5 for mechanisms)

	Mechanisms	Growth rate	Survival	Cover Abundance Density	Recruitment Germination Repr. rate	Associated community: Diversity Abundance	Carbon sequestration
Positive	Reduced turbidity	+		+		+	
	Nutrient enrichment	+		+		+	
	Sulphide metabolism	+	+				
	Sediment stabilization	+	+	+		+	
	Protection from physical disturbance	+	+	+		+	
	Substrate provision			+	+	+	
	Decreased anoxia	+	+				
	Drought resistance		+				
	Protection from seed predation				+		
Negative	Sulphide accumulation	−	−	−			
	Increased epiphyte growth	−		−			
	Space competition	−		−			
	Bioturbation (seed burial)		−		−		
	Increased sedimentation	−			−		
	Higher turbidity	−	−	−			
	Methane production						−
	Smothering		−				

TABLE 4 Positive (+) and negative (−) effects of plants on bivalves (see Figure 6 for mechanisms)

	Mechanisms	Growth rate	Survival	Cover Abundance Density	Recruitment Repr. rate	Condition index	Associated community: Diversity Abundance
Positive	Shelter from predation	+		+	+		
	Increased food availability	+		+		+	
	Substrate provision	+		+	+		+
	Protection from physical disturbance	+	+	+	+	+	
	Sediment stabilization	+	+	+			+
	Drought resistance		+				
	Oxygen production	+					
Negative	Reduced food availability	−	−	−	−		
	Increased predation		−	−			
	Increased sedimentation		−	−	−		
	Space competition		−	−			

4.1 | Seagrass meadows

4.1.1 | Epifaunal bivalves

Within-habitat interactions between seagrasses and epifaunal bivalves are mostly positive, but also context-dependent. Subtidal eelgrass *Z. marina* facilitates blue mussel *M. edulis* and pinnid (Pinnidae) survival and abundance by reducing hydrodynamic disturbances (Aucoin & Himmelman, 2011; García-March, García-Carrascosa, Peña Cantero, & Wang, 2007; Reusch & Chapman, 1995). This may be particularly important for pinnid survival during the first few months post-transplantation when the byssus complex is not fully regenerated (Katsanevakis, 2016). Seagrass shoots can also enhance food supply and facilitate settlement of pinnid larvae

(Aucoin & Himmelman, 2011). However, dense eelgrass can also limit bivalve growth by reducing food supply (Reusch, 1998), suggesting that eelgrass–mussel interactions are context-dependent, varying with shoot density, hydrodynamics and food availability. Studies on scallops (Pectinidae) also show the importance of trade-offs: dense seagrass offers shelter from predators (Carroll, Jackson, & Peterson, 2015; Wolf & White, 1997) and substrate for juveniles (Irlandi, Orlando, & Ambrose, 1999), but limits food availability and growth (Carroll & Peterson, 2013). Scallops may thus select smaller or lower-density seagrass patches (Carroll & Peterson, 2013; Irlandi et al., 1999), where they can benefit from shelter while avoiding food limitations.

The effects of epifaunal bivalves on seagrass show how within- and cross-habitat interactions can differ. In a within-habitat context, mussels can facilitate eelgrass growth by filtering plankton and increasing light availability (Wall, Peterson, & Gobler, 2008), and by fertilizing the sediment through pseudofeces deposition (Reusch, Chapman, & Gröger, 1994). Here again though, context-dependency matters, as in high-nutrient areas, fertilization may instead limit eelgrass growth by increasing epiphyte growth (Vinther & Holmer, 2008; Wagner et al., 2012). Similarly, in areas with organic matter-rich sediments, mussels can instead negatively affect eelgrass by increasing sulphide stress (Vinther & Holmer, 2008). Space competition may also reduce seagrass growth and spread (Wagner et al., 2012). In contrast the cross-habitat effects of bivalve reefs, especially oysters (Ostreidae) are primarily positive, as oyster reefs promote subtidal seagrass growth by filtering water and increasing light availability (Wall et al., 2008), and also allow meadow expansion by reducing wave attenuation (Milbrandt, Thompson, Coen, Grizzle, & Ward, 2015; Sharma et al., 2016).

4.1.2 | Infaunal bivalves

Both positive (González-Ortiz et al., 2016; Peterson, 1982) and negative (Glaspie & Seitz, 2017) correlations have been found between seagrass and infaunal clams such as *M. mercenaria* and *Limecola (Macoma) balthica*. Seagrasses can facilitate clams by providing shelter from predators (Irlandi, 1994) and increased food availability (Irlandi & Peterson, 1991). However, seagrass can also hinder clam growth at high densities (Heck, Coen, & Wilson, 2002) and provide shelter for predators (Rielly-Carroll & Freestone, 2017). Results likely vary due to differences in predator identity and abundance, and seagrass density. Clams promote seagrass growth by increasing light availability (Wall et al., 2008) and nutrients (Carroll, Gobler, & Peterson, 2008).

Infaunal sulphide-metabolizing bivalves (Lucinidae and Solemyidae) play an important role in mitigating sulphide stress in seagrass meadows and mangroves (de Fouw, Govers, et al., 2016; Reynolds, Berg, & Zieman, 2007; van der Heide et al., 2012). Through a symbiosis with sulphide-oxidizing bacteria in their gills (Anderson, 1995), bivalves metabolize sulphides that accumulate in organic matter-rich sediments. As sulphide is toxic to plants (Lamers et al., 2013), they can greatly reduce seagrass mortality, while seagrass provides the oxygen bivalves use to oxidize sulphide (van der Heide et al., 2012) and shelter from predation (de Fouw, van der Heide, et al., 2016).

4.2 | Salt marshes

Cordgrass *Spartina alterniflora* and ribbed mussels *G. demissa*, *G. granosissima* form an important mutualism in salt marshes (Bertness, 1984), in which cordgrass facilitates mussel survival and growth by reducing temperature stress through shading and enhancing food availability. At the same time, mussels facilitate plant growth and survival by providing nutrients and reducing erosion (Bertness, 1984). Oysters can also have positive cross-habitat effects on salt marshes by reducing water turbidity (Wetz, Lewitus, Koepfler, & Hayes, 2002) and stabilizing sediment (Guo & Pennings, 2012). Nearby salt marshes and oyster reefs can also interact to modify hydrodynamic regimes and associated species assemblages (Grabowski, Hughes, Kimbro, & Dolan, 2005). However, within salt marshes, oysters can restrict plant growth (Lomovasky, Alvarez, Addino, Montemayor, & Iribarne, 2014).

4.3 | Mangroves

Most studies in mangroves have been correlative and included both positive and negative interactions. Mangroves can facilitate epifaunal bivalves by providing substrate (prop roots; Aquino-Thomas & Proffitt, 2014), while infaunal sulphide-metabolizing bivalves improve mangrove growth by reducing sulphide stress (Lebata, 2001). Milbrandt et al. (2015) showed that the simultaneous restoration of mangroves and oysters led to an increase in oyster and mangrove abundance, as well as higher invertebrate density on the oyster reef. A local seagrass meadow also expanded in size, likely due to the combined effects of filtration by oysters and substrate stabilization by mangroves.

4.4 | Freshwater SAV meadows

In freshwater systems, interactions between epifaunal bivalves and plants were mostly positive, especially the cross-habitat effects of invasive mussels *Dreissena polymorpha* and *Hyriopsis cumingii*, which promote SAV growth by reducing turbidity and facilitating plant growth (Gao et al., 2017; He et al., 2014; Leisti, Doka, & Minns, 2012; Miehls et al., 2009). Positive within-habitat interactions were also found involving the invasive golden mussel *Limnoperna fortunei*, with plants providing substrate for the mussel (Musin, Rojas Molina, Giri, & Williner, 2015). The infaunal clam *Corbicula fluminea* can also increase water clarity and plant growth, while plants provide refuge from predation (Posey, Wigand, & Stevenson, 1993). However, plants can reduce bivalve growth by increasing sedimentation and reducing food availability (Burlakova & Karatayev, 2007; Posey et al., 1993).

4.5 | General implications for restoration

4.5.1 | Ecosystem services

Successful ecosystem restoration should include re-establishing not only the foundation species, but also the original structure and functioning of the whole community (Shackelford et al., 2013) and associated ecosystem services (Reynolds, Waycott, McGlathery, & Orth, 2016). There is evidence that co-restoring foundation species can facilitate the recovery of associated communities and support higher biodiversity, by increasing the availability of habitats and substrates of differing complexity (Borst et al., 2018). For example, oyster reefs near salt marshes and mangroves support higher densities of invertebrates and piscivorous fish, respectively, than reefs near mud flats (Grabowski et al., 2005; Milbrandt et al., 2015). Oysters on mangrove roots also enhance species diversity by providing additional substrate (Hughes, Gribben, Kimbro, & Bishop, 2014). Within salt marshes, adding mussels can increase biodiversity and trophic network complexity (Angelini et al., 2015; van der Zee et al., 2016). Seagrass also indirectly facilitates higher diversity of pen clam epibiota by increasing clam survival (Zhang & Silliman, 2019). Co-restoration could also restore essential trophic interactions: horse mussels in seagrass beds provided substrate for mesograzers, reducing the epiphytic load on seagrass shoots (Peterson & Heck Jr., 2001).

At smaller scales, microphytobenthos and microbiota play a critical role in regulating processes in vegetated habitats (Brodersen et al., 2018). For example, leaf microbiota of *Posidonia sinuosa* increase nitrogen availability and enhance growth (Tarquinio et al., 2018). Only one study examined the microbial community: Wetz et al. (2002) found that oyster grazing affected the relative abundance of different microbial groups in salt marshes, but how co-restoration affects microbial community dynamics deserves future study.

In addition to biodiversity, successful restoration should also re-establish services such as nutrient cycling and carbon sequestration (McKee & Faulkner, 2000; Reynolds et al., 2016). Many studies addressed how plant and bivalves drive local biogeochemical processes (bivalves increase sediment nutrients and metabolize sulphides, while plants increase oxygen concentrations), but few studies investigated carbon fluxes. Given the role of vegetated habitats as carbon sinks (Alongi, 2012; Fourqurean et al., 2012), fully understanding this aspect of co-restoration should be prioritized.

4.5.2 | Resilience to current and future stressors

Successful restoration should also ensure that restored ecosystems are resilient to environmental factors, especially to climate change. The importance of temperature in driving plant–bivalve interactions suggests that incorporating facilitative positive interactions in subtidal habitat restoration may become more important as global temperatures rise (Bulleri et al., 2018). Correspondingly, it will likely become more critical to consider and avoid negative interactions when restoring intertidal habitats in warmer climates.

4.5.3 | Management of non-native species

Interactions involving non-native species were more likely to be negative than those involving only native species. For example, interactions between *Z. marina* and non-native mussels *Arcuatula (Musculista) senhousia* in the NE Pacific were mostly negative. At high densities, mussels reduced eelgrass growth due to space competition (Reusch & Williams, 1998), while eelgrass reduced mussel growth and survival by limiting food availability and providing shelter for predators (Allen & Williams, 2003; Reusch & Williams, 1999). However, in the NW Pacific where *A. senhousia* is native, dwarf eelgrass *Z. japonica* facilitated the mussel by providing shelter and food (Lee, Fong, & Wu, 2001). A main exception to this pattern was in freshwater ecosystems, where high densities of invasive bivalves benefit plants by filtering water. Efforts should be made to control invasive species populations prior to restoration (Gaertner, Holmes, & Richardson, 2012) and to focus on restoring native species (Sotka & Byers, 2019).

4.5.4 | Context-dependency and the importance of site selection

We focus on the importance of positive interactions, but 15% of studies showed mixed effects (i.e. both positive and negative impacts), and the interactions discussed above show the importance of context-dependency and trade-offs. Incorporation of co-restoration must keep these caveats in mind. In particular, interactions may become negative at high plant densities, at which point they limit food availability for bivalves, or space competition may become an issue. Similarly, co-restoring seagrass and bivalves in eutrophicated areas may instead promote filamentous algae and epiphytes. In most cases, co-restoration is not likely to be a singular solution, and proper site selection is still likely an important determinant for success (van Katwijk et al., 2009). For example, Bos and van Katwijk (2007) found that the initial survival of transplanted eelgrass was higher within an intertidal mussel bed than outside. However, all seagrass eventually died in both locations, showing that reducing external stressors prior to restoration is essential for success.

4.6 | Habitat-specific recommendations

To maximize the potential for positive interactions and enhance restoration success, we have outlined general guidelines for the co-restoration of plants and bivalves in each habitat, while keeping in mind the importance of context-dependency and site-specific conditions.

4.6.1 | Subtidal seagrass meadows

Co-restoration could be beneficial for subtidal seagrasses and bivalves, especially epifaunal bivalves. Small bivalves such as mussels may be most useful in a within-habitat context in exposed, oligotrophic waters where they can fertilize seagrass and stabilize sediment. Larger bivalves such as pinnids may indirectly increase biodiversity by providing additional substrate within meadows. Reef-forming bivalves such as oysters are more useful in cross-habitat configuration, as they can efficiently filter water and attenuate waves. Where sulphide stress is likely to occur, infaunal sulphide-metabolizing bivalves may facilitate seagrass survival.

4.6.2 | Intertidal seagrass meadows

Co-restoration of intertidal seagrasses and epifaunal bivalves could be beneficial, especially in exposed areas where reef-forming bivalves could attenuate waves. In contrast, adding infaunal bivalves within meadows may increase space competition and reduce survival, especially in warmer areas. As in subtidal meadows, an important exception may be sulphide-metabolizing bivalves, which could reduce sulphide stress and increase survival.

4.6.3 | Salt marshes

Co-restoring cordgrass and ribbed mussels will likely increase the survival of both species. In exposed areas, cross-habitat interactions with oyster reefs may also be important for attenuating wave energy and stabilizing sediment. However, within-habitat interactions with oysters and infaunal bivalves are predominantly negative, and should be discouraged.

4.6.4 | Mangroves

Despite a lack of experimental studies, there is potential for co-restoration of mangroves with epifaunal bivalve to accelerate associated community recovery. Adding infaunal sulphide-metabolizing bivalves could also reduce sulphide stress and increase survival.

4.6.5 | Freshwater SAV meadows

Freshwater epifaunal bivalves and plants can facilitate each other, though many studies involved non-native bivalves. In areas where non-native bivalves are present, taking advantage of their potential for increasing water clarity could help plants recover. However, further research should explore whether native species can fulfil the same role.

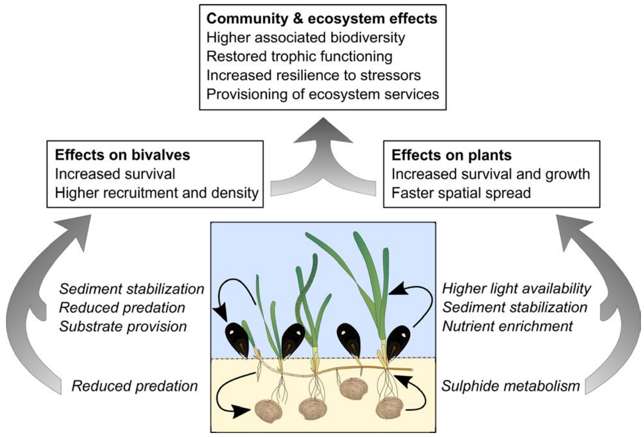

FIGURE 7 Conceptual model of prevailing mechanisms (in italics) by which plant–bivalve co-restoration can facilitate bivalves (left) and plants (right), and the resulting community- and ecosystem-level effects (top). Images represent organism types (plant, epifaunal bivalve and infaunal bivalve), not species. Epifaunal bivalves and plants can also positively affect each other when spatially separated. Images courtesy of Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/)

5 | CONCLUSIONS

Plant–bivalve interactions are important structuring forces in marine and freshwater ecosystems, affecting a suite of variables including species-specific abundance, survival and growth, as well as associated biodiversity and services. Environmental variables, in particular tidal zone and temperature, along with bivalve type, are important drivers in determining the prevalence of positive versus negative interactions. By promoting positive interactions between plants and bivalves, co-restoration could improve restoration success by increasing survival, growth and resilience of foundation species, leading to recovery of associated biodiversity, functioning and ecosystem services (Figure 7). To maximize restoration success, co-restoration strategies should consider species characteristics as well as local environmental conditions in the focal habitat.

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AUTHORS' CONTRIBUTIONS

K.G. and C.B. conceptualized the study; E.R. led the statistical analyses and created the maps and K.G. led manuscript preparation. All authors contributed to the literature search, data extraction and writing, and approved publication of this study.

DATA AVAILABILITY STATEMENT

Data for this review were compiled from papers listed in the Data sources section below.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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