

# RECONCILING RESILIENCE ACROSS ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

Essay Review

Journal of Ecology



## The resilience of coastal ecosystems: A functional trait-based perspective

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### Funding information

This work was supported by the Welsh Government and HEFCW through the 384 Sêr Cymru National Research Network for Low Carbon, Energy and Environment RESILCOAST Project

**Handling Editor:** Roberto Salguero-Gómez

### Abstract

1. Coastal ecosystems provide important services to human population, such as nurseries for fish, carbon storage and coastal protection. However, the pressure faced by these systems due to global changes will strongly challenge the capacity of coastal ecosystems to persist. Therefore, it is crucial to understand the resilience of coastal ecosystems.
2. Here, I propose that combining a resilience framework based on ecosystem properties with the functional trait response–effect framework would allow researchers and managers to quantify the resilience of coastal ecosystems. I place emphasis on salt marsh and sand dunes because of the higher availability of studies for these systems.
3. First, I introduce the resilience framework based on ecosystem properties and, second, I show how adopting a functional trait perspective in this framework would allow researchers to link how environmental changes influence ecosystem properties. In turn, measuring the changes in ecosystem properties would allow researchers to measure the resilience of the system.
4. *Synthesis.* I reviewed several types of disturbances (e.g. storms and sea-level rise) that are threatening the persistence of coastal ecosystems, with an emphasis on salt marshes and sand dunes. Applying this resilience framework reveals, for instance, that the same suite of traits (e.g. plant density and stiffness) increase marsh resistance to multiple threats (e.g. storms and sea-level rise); yet, these traits vary along environmental gradients (e.g. along estuaries) and, therefore, the resilience of marshes vary accordingly. Overall, this framework would allow researchers to gather crucial insights on the resilience of coastal ecosystems and to set reference marks for measuring their resilience under environmental changes.

### KEYWORDS

climate change, coastal ecosystems, environmental gradients, functional traits, plant economic spectrum, recovery, resistance, sea-level rise

[Correction added on 12 April 2021, after first online publication: minor modifications have been applied throughout the paper to improve clarity which do not impact the scientific meaning.]

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## 1 | INTRODUCTION

Coastal ecosystems are greatly important for human well-being because they provide us with a wide range of services (Barbier et al., 2011). For instance, salt marshes, seagrasses and mangroves can store great quantities of carbon, reduce eutrophication and serve as fish nurseries (Barbier et al., 2008; Nelson & Zavaleta, 2012; Ouyang & Lee, 2014; Shepard et al., 2011). Furthermore, coastal ecosystems provide an effective buffer against storms, protecting human infrastructure from damage and potentially saving human lives (Bouma et al., 2009, 2010; Costanza, et al., 2008; Feagin et al., 2010, 2015; Möller et al., 2014; Shepard et al., 2011). Thus, there is a growing interest in managing and restoring coastal ecosystems (Bouma et al., 2014; Feagin et al., 2010, 2015).

Unfortunately, global changes in the current century are expected to have detrimental effects on coastal ecosystems through, for instance, an increase in storm frequency and strength (IPCC, 2019; Woodruff et al., 2013) and sea-level rise (Jevrejeva et al., 2012; IPCC, 2019; Levermann et al., 2013). Moreover, the human population is expected to concentrate along coastal areas (Neumann et al., 2015), which consequently will bring further stress upon coastal systems, for example, destroying natural areas for urban development or altering sediment budgets through the construction of dams. Altogether, human pressure as well as stress from climate change will strongly challenge the ability of coastal ecosystems to persist and deliver their important services (Hanley et al., 2020).

Considering the highly valuable services provided by coastal ecosystems coupled with the current and future threats that these systems are facing (Hanley et al., 2020), it is crucial to gather insights on the resilience (i.e. the ability to persist) of these ecosystems under global changes. In this review, I will, first, introduce the resilience concept based on an ecosystem properties perspective (Oliver et al., 2015) and, second, I will show how this resilience framework will highly benefit from plant trait ecology. Lastly, I will review, through the functional trait lens, the main global changes that could impair the resilience of coastal ecosystems. In this section, I will place emphasis mainly on salt marshes and sand dunes because of the higher availability of studies for these systems. The current gap in knowledge for functional traits on mangrove and seagrasses strongly stresses the need for further research in these systems for fully understanding their resilience.

## 2 | THE RESILIENCE OF ECOSYSTEM PROPERTIES

Resilience is the capacity of an ecological system to persist through time in the face of stress and/or disturbance (Holling, 1973, 1996). Classically, resilience implies that ecosystems exist in two (or more) stable states and it measures the amount of stress that the system can withstand before shifting from one state to another (Beisner, 2012; Carpenter et al., 2001; Scheffer & Carpenter, 2003; Scheffer et al., 2001). Despite being highly popular among researchers and

managers, the resilience concept has branched in multiple meanings (Brand & Jax, 2007) which prevented standardising methods for its quantification (Beisner, 2012; Myers-Smith et al., 2012).

Recently, however, a more practical approach to resilience has been proposed (Oliver et al., 2015). In this approach, the focus lies on the functioning/properties of ecosystems because they underlie key services provided to human populations (e.g. coastal protection and food production). In this approach, the resilience of an ecosystem property can be divided into two complementary aspects, the resistance to, and recovery from, stress/disturbance, where disturbances can be grouped in three main categories depending on the time-scale they act: pulse, chronic and rapid-onset (Oliver et al., 2015). For instance, a storm impacting a sand dune is a transitory (pulse) disturbance, where waves hit the foredune for few hours or days, possibly leading to severe erosion (Pye & Blott, 2008; Roberts et al., 2013). Eutrophication in coral reefs is an example of a (relatively) low but steady increase in disturbance (chronic), where the constant nutrients discharge into the water boosts algae proliferation which could lead to a shift from a coral dominated to an algae-dominated state (Hughes, 1994). Lastly, land reclamation in salt marshes for urban development or agriculture is an example of rapid-onset disturbance (Adam, 2002; Feagin et al., 2015), where a strong disturbance sharply affects the system and remains constant through time. Overall, understanding the resilience of ecosystem properties implies to unravel the mechanisms that enable these properties to resist and recover from those different types of disturbance/stress.

## 3 | A FUNCTIONAL TRAIT APPROACH TO RESILIENCE

According to Violle et al. (2007), a trait is a '*morpho-pheno-physiological feature measurable at the individual level, from cell to the whole organism, without reference to the environment or any other level of organisation*'. A central tenet in plant trait ecology is that species display traits that enable individuals to survive and reproduce in a given environment (Garnier et al., 2016; Westoby et al., 2002). Traits can be distinguished between response traits, those that respond to environmental changes, and effect traits, those that influence ecosystem properties (Lavorel & Garnier, 2002). As an example, in nutrient-rich soils, plant communities adopt traits, such as high specific leaf area and nitrogen content, and low tissue density, for fast resource acquisition; in turn, this strategy allows plants to grow quickly, leading to high net primary production (Lavorel & Garnier, 2002). Thus, the trait approach can allow us to mechanistically link the effects that environmental changes have on organisms (traits), scaling it up to communities and, in turn, to ecosystem properties (Lavorel & Garnier, 2002; Lavorel et al., 2013; Suding et al., 2008).

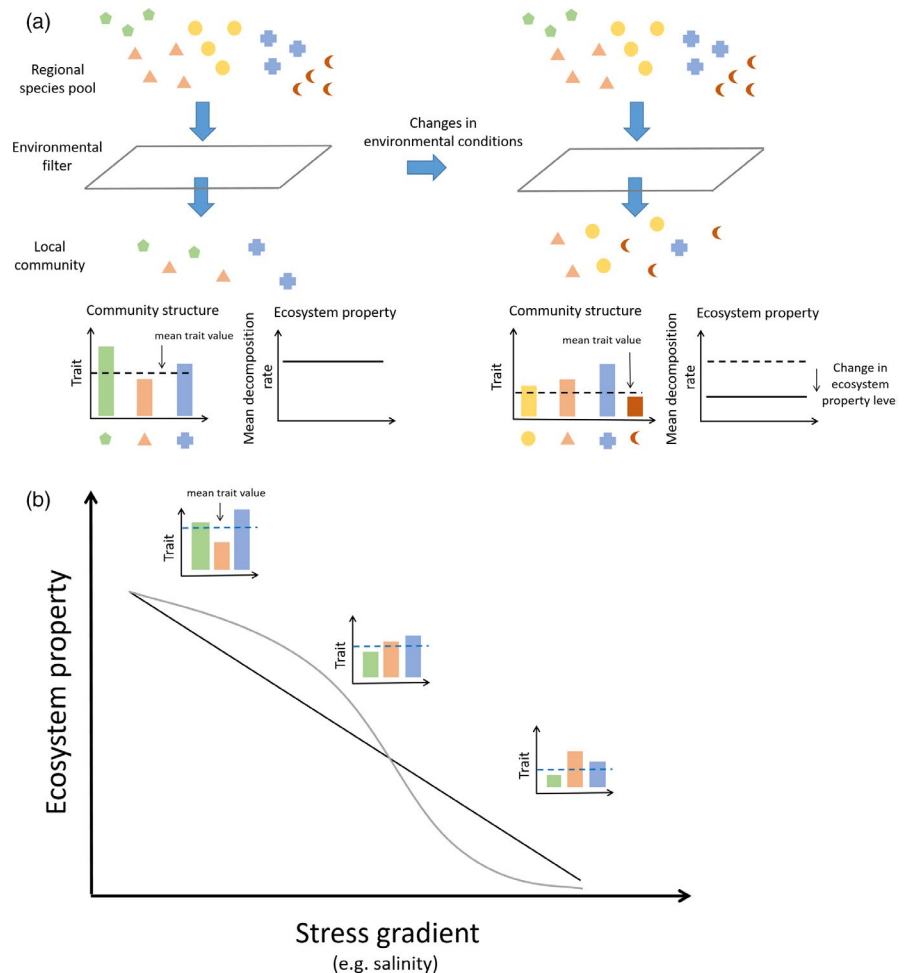
Studies in trait ecology have demonstrated that plants exhibit suites of correlated traits, such as the plant economic spectrum (PES; Díaz et al., 2016; Garnier et al., 2016; Laughlin, 2014; Westoby et al., 2002; Westoby & Wright, 2006). Along with the PES, species display traits in a continuum from fast resource acquisition and

rapid growth to resource conservation and slow growth (Freschet et al., 2010; Reich, 2014; Reich et al., 1997; Wright et al., 2004). Traits changes along with the PES have important consequences for ecosystem properties and services. For instance, in a sub-arctic flora species with a conservative strategy produce litter that decomposes slower than that of species with an acquisitive strategy, ultimately slowing down nutrient cycling (Freschet et al., 2010). Thus, the PES theory could be effectively used for mechanistically linking how variation in ecosystem properties reflects the changes in environmental factors.

Interestingly, plant economic strategies might underpin how species or communities resist—and recover from—environmental changes or stresses. As an example, the seagrass *Posidonia oceanica* is a species highly resistant to heat, hypoxia and salinity stress, because of the high reserves stored in its rhizomes (Unsworth et al., 2015); on the other hand, this species grows slowly and thus a degraded meadow needs decades or centuries for recovering after a disturbance (Gonzalez-Correa et al., 2005; Marbà & Duarte, 1998). In contrast, the seagrass *Halophila* sp. has low ability to resist to stress, but can recover rapidly from disturbance because of its high seed production, the presence of a seed bank and fast growth (Unsworth et al., 2015). Thus, this example might suggest that species investing in traits which enable plants to resist stress but recover slowly might have a conservative plant economic strategy while species with traits that enable plants to quickly recover from stress might

have an acquisitive strategy. It is worth noting that similarly to plant economic strategies, Grime (1977) proposed a classification of plants in competitor-stress tolerant-ruderal (the C-S-R scheme). In this scheme, he identifies as stress-tolerant those species which are capable to resist stress by investing in retaining resources and in dense, persistent tissue and as competitor those plants capable to quickly acquire resources and grow fast (Grime et al., 1977; Pierce et al., 2017). Yet, at present, we still poorly understand whether traits related to stress resistance and recovery actually align with plant strategies or Grime's competitor and stress-tolerant categories. Overall, understanding whether traits related to stress resistance and recovery form independent suite of traits is fundamental for gaining knowledge on the resilience of ecosystem properties under current and future global changes.

Adopting this functional traits perspective into the resilience of ecosystem properties (and their associated services) has appealing consequences: it allows researchers to mechanistically understand how changes in the environment will affect the resilience of the system and to set clear reference points against which to evaluate resilience. As an example, an environment selects for a plant community with a determinate structure (i.e. species traits) which has an associated level of an ecosystem property (e.g. high plant litter decomposition, left-hand side in Figure 1a; Freschet et al., 2012, 2013; Garnier et al., 2016; Laughlin et al., 2015). A change in the environment, due



**FIGURE 1** Panel (a), conceptual model about how environmental changes due to pulse, chronic or set disturbances lead to a shift in community structure and, in turn, to ecosystem properties and associated services. On the left-hand side, starting environmental conditions select for a plant community with determinate trait(s) values which, in turn, provide for a certain level of an ecosystem property (e.g. decomposition). In the right-hand side, new environmental conditions lead to a change in the plant community trait(s) that determines deterioration of the ecosystem property (i.e. decomposition). Panel (b), example about how communities traits vary along a stress gradient (e.g. salinity) and, as consequence, also the ecosystem properties and their resilience vary accordingly. Note that the ecosystem property can change either linearly (black line) or not (light grey line) along the gradient

to either a sharp (pulse/rapid-onset) or chronic disturbance, will select for a different plant community structure which, in turn, can reduce the associated ecosystem property level (e.g. low plant litter decomposition, right-hand side in Figure 1a; Freschet et al., 2012, 2013; Garnier et al., 2016; Laughlin et al., 2015). Thus, through this trait-based approach, we could evaluate if the new level of the ecosystem property could underlie a degradation of the ecosystem services provided (e.g. nutrient cycling), and, importantly, we could measure the amount of change, that is, resilience, that the system has experienced. Therefore, this resilience approach focusing on ecosystem properties and adopting a trait-based perspective would allow researchers to understand and measure the changes that (coastal) ecosystems will experience under global changes.

Furthermore, adopting this trait-based approach focused on ecosystem properties highlights another important aspect of resilience which is rarely considered but crucial for resilience's management: ecosystem properties naturally vary along environmental gradients and, therefore, their resilience might naturally vary as well. As an example, high salinity in salt marshes induces plants to adopt traits (e.g. low leaf area and stem density; Naidoo et al., 2008; Qiu et al., 2008) that ultimately reduce the capacity of marshes to resist wave action (Bouma et al., 2013). Therefore, marshes under higher salinity stress, such as at estuary mouths (De Battisti et al., 2019) and lower latitudes (Bertness et al., 1992), could have intrinsic low resilience. This implies that some marshes are more vulnerable to some type of disturbances than others (e.g. marshes at the mouth of the estuary might suffer from increments in salinity due to rising temperature under climate change; Figure 1b). Furthermore, the restoration of different marshes cannot have the same goal in terms of ecosystem properties (and services) level to achieve because of the different starting resilience points.

I stress that focusing on the resilience of ecosystem properties would still benefit from the concepts of multiple stable states for understanding ecosystem dynamics (Holling, 1996; Scheffer et al., 2001). However, this ecosystem property perspective is not tied to threshold points and the long time series needed for detecting them, meaning that it can be applied also in systems regardless of the presence (or absence) of multiple states. Therefore, this resilience approach can be applied to a wide range of situations, allowing managers to set clear management and restoration goals.

## 4 | TRAIT-BASED RESILIENCE IN COASTAL ECOSYSTEMS

In this review, I focused on coastal ecosystems because of the highly valuable services they provide to human well-being. Unfortunately, coastal ecosystems are not equally well studied and, in particular, the application of the trait-based approach is still in its infancy in these systems. Thus, this review is timely and appropriate for unravelling the strength of the trait-based approach for understanding the functioning of coastal ecosystems and to gather insights on their resilience. On the other hand, because of the scarcity of trait-based

studies in these systems, I have placed particular emphasis on salt marshes and sand dunes.

In the following sections, I have identified several stresses belonging to each of the three types of disturbance previously identified (pulse, chronic and rapid-onset) which are known for threatening the persistence of coastal ecosystems. I then reviewed what is currently known about the capacity of coastal systems to resist these threats. In particular, I have mainly focused on plants' ability to bind the sediment because this is a vital function that enables sediment dominated coastal ecosystems to exist.

### 4.1 | Resistance to pulse disturbances

#### 4.1.1 | Storminess

Extreme weather events such as hurricanes and tsunamis have strongly increased our awareness on the importance of coastal ecosystems for coastal defence (Costanza et al., 2008; Feagin et al., 2010; Shepard et al., 2011). Vegetation strongly influences the coastal protection capacity of these systems thanks to its ability to dampen wave energy and stabilise the sediment, acting as a first barrier against waves and storm surges (Bouma et al., 2014; Costanza et al., 2008; Feagin et al., 2010, 2015, 2019; Hanley et al., 2020; Shepard et al., 2011; Silva et al., 2016). For instance, field observations showed that mangrove forests can reduce shore erosion up to 15 times in comparison with unvegetated shores (Sánchez-Núñez et al., 2019), while seagrass meadows can reduce the wave height reaching the shore up to 50% (Infantes et al., 2012). Similarly, flume studies (a flume is a laboratory facility that allows to generate waves and/or water currents of desired intensity) in salt marshes and sand dunes demonstrated that vegetation can reduce erosion rate up to 80% (Lo et al., 2017) and 36% (De Battisti & Griffin, 2019) respectively. Therefore, understanding the mechanisms by which vegetation ensures sediment stability is crucial for gaining insights on the resilience of coastal ecosystems.

The vegetation's capacity to reduce wave energy and to bind the sediment is related to several plant traits. Above-ground, vegetation biomass exerts a friction on water (or wind) flow which reduces flow-induced erosion (e.g. Bouma et al., 2013). Yet, the strength of this flow reduction varies with plant traits: in salt marshes, tall species with stiff stems, such as *Spartina anglica*, are the most effective in reducing water flows, whereas the shorter, softer species as *Puccinellia maritima* and *Salicornia procumbens* are less effective (Bouma et al., 2013). Similarly, in sand dunes, high vegetation cover effectively reduces the wave swash because shoots and leaves dissipate wave energy through friction (Silva et al., 2016); this is further supported by a recent study in sand dunes where plants with higher leaf number had a stronger effect on reducing sediment erosion (Feagin et al., 2019). Furthermore, these studies showed that plant density is a key aspect of erosion resistant, pointing out that traits related to plants' clonal growth are crucial for the resistance of ecosystem properties to disturbance, although this aspect is less studied (Cornelissen et al., 2014). Indeed, a flume study with clonal marsh plants showed

that *P. maritima* patches were as effective as *S. anglica* patches in reducing the water flow thanks to their higher shoot density (Bouma et al., 2010). Overall, environmental factors that favour a community structure with taller, stiffer or more dense vegetation would increase the resistance aspect of resilience against wave action.

Regarding sediment stability, studies have found that two main factors drive sediment erosion and they act antagonistically: sediment grain size and vegetation root biomass (De Battisti et al., 2019; Lo et al., 2017). Sand content can strongly influence erosion rates (De Battisti et al., 2019; De Battisti & Griffin, 2019; Feagin, 2009) because sand (i.e. big grain size) erodes much easier than clay (i.e. small grain size; Schutten et al., 2005). Thus, a system with high sand content (e.g. sand dunes) has a low capacity to resist disturbance in comparison to a system with higher clay content (e.g. salt marshes). However, root biomass binds the sediment together, counter-acting sediment erosion (De Battisti et al., 2019; De Battisti & Griffin, 2019; Ford et al., 2016; Lo et al., 2017). Indeed, recent flume studies both in salt marshes and sand dunes found that below-ground biomass effectively stabilises sandy sediments (De Battisti et al., 2019; De Battisti & Griffin, 2019; Ford et al., 2016; Lo et al., 2017), highlighting the pivotal role of vegetation where it is more needed. Altogether, these studies indicate that, at a same grain size, below-ground biomass confers stronger resistance to disturbance, that is, improves the resilience of the system.

Interestingly, a study with seagrasses indicates that plants' ability to reduce wave/water energy above-ground is likely in trade-off with their capacity to anchor the plants in the soil (Infates et al., 2011). In this study, *Posidonia oceanica* plants experienced higher drag forces by water currents than *Cymodocea nodosa* plants due to their bigger leaf surface area; as a consequence, *P. oceanica* plants need a greater root biomass (~40% of total biomass) to resist up-rooting at same currents strength in comparison to *C. nodosa* (~20% of total biomass). Thus, understanding which factors influence the above- to below-ground biomass investment will highly improve our understanding about how resilience varies within ecosystems.

The PES theory can help us to unravel how trade-offs in above- to below-ground biomass investment drive the resilience of coastal ecosystems. The PES theory indicates that plants in nutrient-rich soil adopt an acquisitive strategy and produce cheap, nutrient-rich tissue (e.g. specific leaf area and specific root length), that increases above-ground primary production (Freschet et al., 2010, 2012; Reich et al., 1997, 1999; Reich, 2014; Wright, 2004). At the same time, a greenhouse study with alpine trees showed that plants with an acquisitive strategy invested less in root mass fraction (Freschet et al., 2015). Therefore, we could expect that also for coastal systems a shift in plants traits towards an acquisitive strategy would, on the one hand, increase above-ground biomass production and thus the resistance of ecosystem properties against wave energy but, on the other hand, reduce the root mass fraction and thus the resistance of ecosystem properties against sediment erosion. However, a recent study in salt marshes gives a more complicated picture. In *Spartina anglica*, strong abiotic stress (high salinity and low sediment redox) independently controlled different plant traits which influenced

above- and below-ground biomass investment: high salinity leads plants to adopt a more conservative strategy which increased the below-ground investment; while higher sediment redox leads plants to produce more coarse roots and, in turn, more above-ground biomass (De Battisti et al., 2020). Thus, the overall net effect on the ecosystem properties capacity to resist wave energy dissipation and sediment stabilisation would depend on the salinity and redox levels experienced by plants. This result highlights the importance of considering multiple abiotic stressors and suite of traits to fully understand the resilience of ecosystem properties.

#### 4.1.2 | Temperature increase and drought

Extreme events such as high temperature and drought act on short-term scales (days to months) and can be considered as a pulse disturbance. These stresses are expected to increase under current climate change (IPCC, 2019): for instance, simulations of extreme heat events, under the scenario of +3.5°C on average at global scale, have forecast temperatures exceeding 40°C degrees before 2,100 over much of the United States and southern Europe (Sterl et al., 2008). Therefore, understanding how high temperature and drought will impact coastal ecosystems, in general, is of crucial importance if human populations want to continue benefiting from the services provided by these systems.

Temperature increments can have detrimental effects on the survival of ecosystems. In salt marshes and seagrasses, a high temperature leads to an increase in water evaporation and thus salinity, which can impact plants' survival (Bertness et al., 1992; Crain et al., 2004; Gedan et al., 2011; Watson & Byrne, 2009). Furthermore, increasing temperature and salinity can drive changes in plant communities (Baldwin & Mendelssohn, 1998; Gedan et al., 2011; Watson & Byrne, 2009) which may alter ecosystem properties if the new community display different suites of traits (Hanley et al., 2020).

Plants living in coastal areas have developed several traits to cope with drought and salinity stress. For instance, *Cakile maritima* (sand dunes), *Atriplex portulacoides* and *Salicornia europaea* (salt marshes) adopted succulent leaves for maintaining osmotic balance under water deficit or saline conditions (Flowers & Colmer, 2008). Another mechanism for regulating osmotic balance is to produce secondary metabolites like proline (Flowers & Colmer, 2008; Slama et al., 2015; Tabot & Adams, 2013, 2014). In salt marshes, plants produce aerenchyma for coping with waterlogging (Colmer, 2003; Colmer & Flowers, 2008; Justin & Armstrong, 1987). Interestingly, aerenchyma production has also been related to drought resistance, because an increment in the percentage of dead cells, of which aerenchyma is formed, determines a decrease in metabolic requirements and, thus, water requirements (Zhu et al., 2010). This result suggests that traits related to resistance to one stress (e.g. waterlogging and salinity) might underpin the ability to resist to another stress (e.g. drought). Thus, different disturbance types (e.g. sediment redox and drought) might lead to similar changes in

plant traits (e.g. aerenchyma production) and consequently have a similar effect on the ecosystem properties resilience (e.g. plants capable to produce aerenchyma should also be more resistant to drought stress). Overall, future studies should consider how changes in a suite of traits for resistance to one stress are related to other stress types, ultimately influencing the resilience of ecosystem properties.

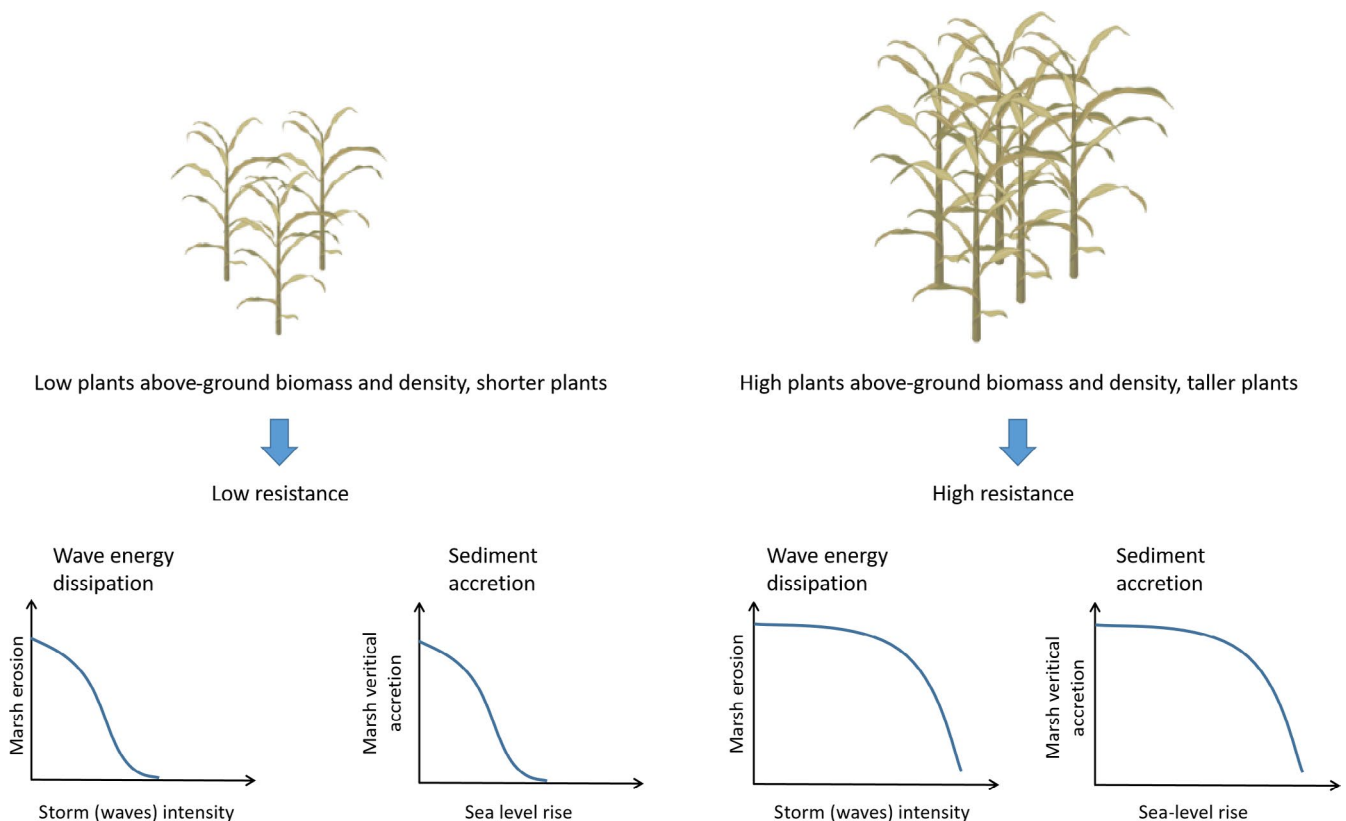
## 4.2 | Resistance to chronic disturbance

### 4.2.1 | Sea-level rise

Sea-level rise, due to ice melting and thermal expansion under global warming, is considered as an important threat for coastal ecosystems (Hanley et al., 2020; IPCC, 2019). The effect of sea-level rise on coastal ecosystems depends on several factors that operate at the local level, such as land isostatic adjustment and sediment availability (Adam, 2002). For instance, salt marshes on the South-East coast of the UK have experienced higher marsh loss in the past decades because of both land subsidence and a shortage of sediment supply; in contrast, marshes on the West coast have remained constant or accreted for the opposite reasons (Adam, 2002; Ladd, 2018). Several studies have shown the importance of sediment availability for the survival of coastal ecosystems

(D'Alpaos et al., 2007; Kirwan et al., 2010; Saintilan et al., 2020). For instance, marshes and mangroves can withstand high rates of sea-level rise if enough sediment for accretion is supplied (D'Alpaos et al., 2007; Kirwan et al., 2010, 2016; Kirwan & Murray, 2007; Saintilan et al., 2020). The capacity of these systems to adjust to sea-level increments arises from plants' ability to slow down water flow, consequently increasing sediment deposition and, thus, the vertical accretion of the system (see Bouma et al., 2009, 2010, 2013; Cahoon & Lynch, 1997; Krauss et al., 2014). This feedback process of sediment deposition and accretion ultimately allows salt marshes and mangroves to withstand sea-level rise (D'Alpaos et al., 2007, 2012; Kirwan et al., 2010; Saintilan et al., 2020). Altogether, these studies strongly highlight the importance of vegetation to resist sea-level rise.

Interestingly, flumes, modelling and field studies have investigated the capacity of salt marsh plants to reduce water flow and increase particle sedimentation (e.g. Bouma et al., 2007, 2010, 2013; Duggan-Edwards et al., 2019). These studies showed that traits responsible for sediment accretion, that is, plant height, stiffness and density, are also involved in wave energy dissipation. In other words, marshes with taller and stiffer plants at higher density will not only have a stronger resistance to storms but will also have a stronger resistance to sea-level rise (Figure 2). These results further indicate that the same suite of traits can underpin the ecosystem properties resistance to multiple stress.



**FIGURE 2** Example in salt marshes about how the same suite of plant traits (e.g. plant density, stiffness and above-ground biomass) influences the ecosystem properties resistance to multiple stress type (e.g. wave energy and sea-level rise). Drawings of plants were created in BioRender.com

#### 4.2.2 | Long-term temperature increments

In addition to drought (high temperature for a short time), global warming acts also over a long period and, thus, can be regarded as a chronic disturbance. Long-term warming can alter plant communities (Gedan et al., 2011; Watson & Byrne, 2009) which, displaying a different suite of traits, might change ecosystem properties and their associated services (e.g. coastal protection and carbon sequestration). As an example, under higher salinity due to long-term temperature increments, salt-tolerant marsh plants have expanded at the expense of not-tolerant species (Watson & Byrne, 2009). The consequences of this species replacement will depend on the new species traits: in case high productive species will replace low productive ones (e.g. *Scirpus maritimus* replaces *Distichlis spicata*; Watson & Byrne, 2009), then resilience could be enhanced (i.e. higher biomass production provides better resistance against waves erosion; e.g. Figure 2). In contrast, if new species display traits less effective against disturbances (e.g. the smaller *Salicornia virginica* replaces the taller *Spartina foliosa*), then the resilience of the system could be hampered. At present, however, we still poorly understand how changes in plant community traits under global warming will affect ecosystem properties in coastal systems and, thus, their resilience.

The trait-based approach can help us to gain insights on the consequences that changes in community traits have on ecosystem resilience. For instance, in Eastern US sand dunes, warming led the dune-builder *Uniola paniculata* to expand northward, replacing another dune-builder, *Ammophila breviligulata* (Goldstein et al., 2018). These two species differ in their clonal growth, with *A. breviligulata* producing more clumped shoots and having faster later spread with respect to *U. paniculata*; in turn, *A. breviligulata* forms taller, wider foredunes. Thus, considering that taller, wider foredunes provide higher coastal protection (Pries et al., 2008), the northward expansion of *U. paniculata* at the expanses of *A. breviligulata* might reduce sand dunes' resistance to storms and, therefore, their resilience. Overall, the trait-based approach can provide us valuable insights on the resilience of ecosystem properties under global changes.

#### 4.3 | Resistance to rapid-onset disturbance

Land reclamation can be considered as a rapid-onset disturbance, which has affected coastal ecosystems (Barbier et al., 2011; Feagin et al., 2015). In salt marshes, land reclamation typically consists in building a dam in front of the marsh to create new land where to grow crops or create new pasture for cattle and/or sheep (Adam, 2002; Allen, 2000). In sand dunes, urban development for recreational purpose is an example of land reclamation (Barbier et al., 2008, 2011; Feagin et al., 2015). In these cases, because the natural environment is actively destroyed by human intervention, little can be done by vegetation to resist to this type of disturbance. Thus, when dealing with rapid-onset disturbances, it is more appropriate to focus on the removal or mitigation of the disturbance itself and on the capacity of the system to recover.

## 5 | RECOVERY

The ability of plant communities to recover after a disturbance is fundamental for understanding the resilience of coastal ecosystems. In this section, I highlight the principal mechanisms of vegetation recovery in coastal ecosystems, both from seed germination and vegetative re-growth, with an emphasis on the associated traits. Again, I have mainly placed emphasis on salt marshes and sand dunes because of the higher availability of studies for these systems.

### 5.1 | Recovery from seeds

A key mechanism for recovery after disturbance is seed recruitment, which allows plant dispersal, regeneration and gene flow (Traveset et al., 2014). In wetlands, seagrasses and mangroves, the main agent of seed dispersal is water, but wind and animal dispersal are also important (Kendrick et al., 2012; Neff & Baldwin, 2005; Van der Stocken et al., 2019). In sand dunes, wind is the main dispersal agent in foredunes, although water could also be important for pioneer species such as *Cakile* spp. (Maun, 2009). Traits underlying the seed dispersal capacity seem to depend upon the length, width and mass of the seed (Erfanzadeh et al., 2010; Traveset et al., 2014). In water, small seeds are thought to have high dispersal capacity thanks to their ability to float for a long period (Erfanzadeh et al., 2010). Indeed, the pioneer species *Salicornia europea* and *Suaeda marina* have small seed size and are the first to colonise mudflats in newly restored salt marshes (Erfanzadeh et al., 2010; Mossman, Brown, et al., 2012; Mossman, Davy, et al., 2012). However, other studies on the colonisation of restored marshes have found that seed weight was not a good predictor of dispersal for the same two species (Wolters et al., 2005, 2007). Moreover, in seagrasses and sand dunes, higher fruit mass is considered as an adaptation for water dispersal (Maun, 2009; Orth et al., 2006). Altogether, seed size and length are important traits for seed dispersal but other traits likely play a conspicuous role for seed dispersal.

A persistent seed bank in the soil is an important factor for vegetation recolonisation after disturbance (Huiskes et al., 1995). Although this is true for some species (e.g. the seagrass *Halophylla* spp.; Kendrick et al., 2012; Orth et al., 2006), in coastal systems many species lack persistent seed bank (Caldwell, 2008; Maun, 2009; Unsworth et al., 2015; Zhu et al., 2014). In this latter case, recolonisation after disturbance strongly depends on propagules exported from near intact sites (Erfanzadeh et al., 2010; Wolters et al., 2005, 2007). In salt marshes, for instance, studies showed that many seeds are exported from the pioneer zone with the ebb tide (Huiskes et al., 1995) and that 'donor' sites are crucial for marsh recovery (Wolters et al., 2005, 2007). Importantly, Erfanzadeh et al. (2010) reported that species which colonised a restored marsh first were not the most abundant species at the 'donor' site. This result suggests that the capacity of marsh recolonisation is not only dependent on seeds recruitment from other marshes but also on the species identity, and thus traits, of the incoming seeds. Further research is

strongly needed to elucidate the role of connectivity among coastal systems, as seed donor sites might play an important role in recovery.

Regarding plant ecological strategies, a trade-off in seed mass with seed number would underpin the plants' ability to colonise wide areas (high seed number with low biomass) or to germinate and survive in a stressful environment (low seed number with higher biomass; Westoby et al., 2002). This trade-off would exist because high nutrient reserves in seeds with higher mass would allow seedlings to grow in a stressful environment; however, the higher mass investment per seed would limit the seed production by the parental plant (Westoby et al., 2002). Thus, according to this ecological strategy, we should expect that plant species with many small seeds would lead to a quick recolonisation. However, this theory only partially applies to salt marshes and sand dunes. In salt marshes annual species produce abundant, small seeds and indeed were the first to colonise restored sites (Erfanzadeh et al., 2010; Wolters et al., 2005, 2007); yet, they do so despite the mudflat is a harsh environment for plant colonisation (Bertness & Ewanchuk, 2002; Bertness et al., 1992; Davy et al., 2011). In sand dunes, bigger seeds allow plants to better survive burial stress (Maun, 2009). However, the annual forb *Cakile maritima* produces fruits of two sizes among which the bigger one, with bigger seeds, is easily detached from the plants and is related to plant long-distance dispersal by water (Maun, 2009).

To reconcile this discrepancy, it must be considered that this ecological strategy has been developed in terrestrial ecosystems (Westoby et al., 2002). Thus, specific adaptations to intertidal-aquatic environments could have altered this ecological strategy. Specific physiological plant adaptations for coping with harsh environments, such as the mudflat, or adaptation for dispersal (e.g. buoyancy in water) would possibly alter the seed mass-number trade-off. On the other hand, stochastic events might also play a crucial role in seed germination and, thus, recovery. Studies have shown the existence of Windows of Opportunity in coastal systems (Balke et al., 2011, 2013), where stochastic events lead to a reduction in environmental stress (e.g. lower mean tide level) with consequent large recruitment and germination of plant seeds (Balke et al., 2013; Hu et al., 2015). As an example, an eroding salt marsh in the Netherlands was able to 'bounce back' several meters thanks to a temporary drop in mean water level for few years which increased seedlings survival (Balke et al., 2013). Overall, more studies are needed to understand which seed (and plant) traits underpin the capacity of salt marsh and sand dune systems to recover after disturbance and how these traits relate to the plant ecological strategies.

## 5.2 | Recovery from vegetative re-growth

Although seed production is the main mode of recruitment for annual plants, several perennial foundation species in salt marshes, sand dunes and seagrasses depend on vegetative re-growth (Wolters et al., 2007; Maun, 2009; Marbá & Duarte, 1998). For instance, plants such as *Spartina alterniflora* (salt marsh) and *Ammophila arenaria* (sand dune) do have high seed production, but

recruit principally by vegetative re-growth (Angelini et al., 2016; Maun, 2009). Interestingly, a study in a restoration project showed that perennial plants, such as *Puccinellia maritima*, *Atriplex portulacoides* and *Spartina anglica* had a sigmoidal curve of appearance, with an initial low recruitment period followed by an intense expansion in a relatively short time (Wolters et al., 2007). This behaviour has been linked to the clonal growth of these plants, where large clonal patches produce more new individuals in a given time with respect to small patches (Wolters et al., 2007). Thus, plants' clonal growth could have strong influence over the recovery of ecosystem properties and thus, their resilience.

Plants' clonal growth can be described by several traits, such as rhizome elongation rate, internode lengths and branching angle (Cornelissen et al., 2014). In seagrasses, a study showed that differences in rhizome elongation rate and branching angle lead to different clonal growth type: a guerrilla type, as in *Posidonia oceanica*, and a phalanx type, as in *Halophila ovalis* (Marbá & Duarte, 1998). In the guerrilla growth type, plant's rhizomes elongate faster and have wider branching angle, leading to the formation of a sparser clone (Cornelissen et al., 2014; Marbá & Duarte, 1998). A recent study in sand dune found that a clumped growth allows *Ammophila arenaria* to trap sediment better than the sparse growth form of *A. breviligulata* (Reijers et al., 2019). In turn, these clonal growth differences lead species to occupy larger or smaller areas and, therefore, having higher or smaller recovery in term of the space occupied (e.g. at comparable rhizome length *P. oceanica* occupies larger areas with respect to *H. ovalis*). Moreover, considering that plant density and vegetation cover are related to waves dissipation (e.g. Infantes et al., 2012; see above) and sediment accretion (Bouma et al., 2009, 2013; see above), traits related to clonal growth (e.g. guerrilla or phalanx) might have strong consequences on the resilience of the system. Yet, at present, we still poorly understand how clonal traits relates to ecosystem properties resilience.

## 6 | MANAGEMENT IMPLICATIONS AND FUTURE DIRECTIONS

The resilience approach, highlighted in this review, can help managers to define clear, quantitative references for resilience. In Table 1, I give an example for salt marshes regarding the effect of salinity (abiotic factor) on plant traits and, in turn, the effect of traits on soil stability (ecosystem function). For instance, in salt marshes at increasing salinity levels, plant species produce smaller leaves (low leaf area, LA), less stiff shoot, and less shoot biomass (response traits). These traits interact with wave and water flow, reducing marsh erosion and increasing sedimentation (Bouma et al., 2009, 2013; Duggan-Edwards et al., 2019). Therefore, reduction in LA, stiffness and biomass with increasing salinity will decrease plant capacity to reduce wave/flow energy and thus to resist soil erosion. Moreover, sediment stability depends on root density and on the amount of sand present in the sediment (Table 1; De Battisti et al., 2019). Sand content and root density vary depending on the zone and species



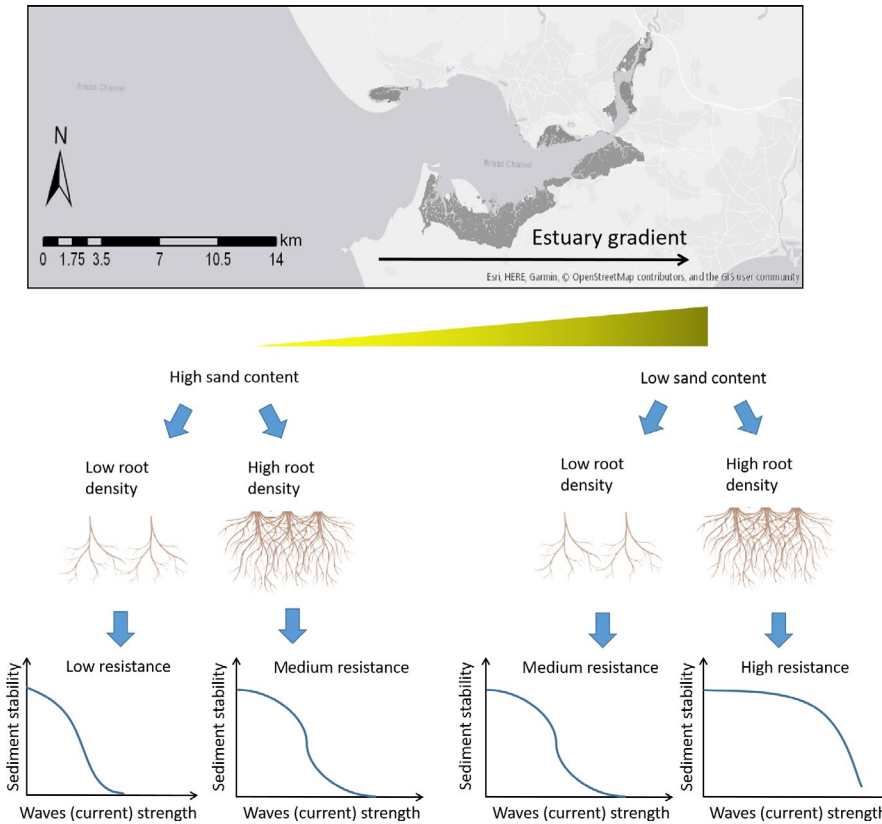
**TABLE 1** Hypothesised effect based on literature of an environmental factor (salinity) on plant traits and the effect of traits on an ecosystem function (soil stability). In turn, hypothesised effect of traits on resilience (resistance and recovery). Arrows pointing upward indicate a positive effect; arrows pointing downward indicate negative effect; arrows pointing to the right indicate possible positive and negative effect. Question marks indicate unknown effect

Abiotic environment (e.g. salinity)		Ecosystem property (e.g. soil stability)		Resilience	
Effect on plant traits	Trait	Mechanism	Trait effect on soil stability	Resistance	Recovery
	<i>Leaf</i>				
↓	Leaf area (LA)	Waves energy reduction	↑	↑	?
↑	Specific leaf area (SLA)	Wave/flow energy reduction	→	→	?
↓	Leaf dry matter content (LDMC)	Wave/flow energy reduction	↑	→	
	<i>Stem</i>				
↑	Stiffness	Wave/flow energy reduction	↑	↑	→
?	Specific stem density (SSD)	Increase resistance to breakage	↑	↑	→
↓	Stem C/N	Increase resistance to breakage	↑	↑	→
→	Shoot density	Wave/flow energy reduction	↑	↑	↑
↓	Shoot biomass	Wave/ flow energy reduction	↑	↑	↑
	<i>Roots</i>				
↓	Root density (RD)	Increase soil cohesion	↑	↑	↑
↓	Root length density (RLD)	Increase soil cohesion	↑	↑	↑
?	Root depth	Increase soil cohesion and plant anchorage	↑	↑	?
→	Root biomass	Increase soil cohesion	↑	↑	↑

considered, for example, low or middle marsh zone, and on the marsh position along an estuary, for example, head or mouth of the estuary (De Battisti et al., 2019). Therefore, knowing the values of these variables would allow us to draw maps of marsh resistance to erosion, both within and across marshes (Figure 3). These maps could also be used as a reference for a future assessment of marsh resistance to erosion. For instance, in the future, the species composition will change in these marshes due to changes in the environment (e.g. salinity), the new values found for root density and sand content could be compared with the previous one and, therefore, it could be determined if the marsh resistance to erosion has deteriorated, increased or maintained. Overall, these examples show how useful and practical this trait-based resilience approach can be for research and management purposes.

Furthermore, in this review, I have mainly focused on traits that are both response and effect traits, that is, traits that respond to environmental changes and affect ecosystem properties, respectively (Lavorel & Garnier, 2002). The aim was, first, to highlight the

benefits of incorporating the trait-based approach into the resilience framework and, second, to provide insights on the resilience of ecosystem properties to several threats well known for coastal systems. However, response traits are not necessarily effect traits and thus, having a direct influence over ecosystem properties (Lavorel & Garnier, 2002). Nevertheless, a recent study indicates that species with different combinations of pure response traits can coexist under the same environmental conditions, ultimately influencing ecosystem properties (Dias et al., 2020). For instance, in Brazilian sandy coastal plains, tree species coexisted under low water availability thanks to the combination of different levels of wood density, leaf succulence and minimum leaf water potential (Rosado & de Mattos, 2017). In turn, because these species have different leaf tissue composition (which is related to leaf decomposability), then they potentially have a contrasting effects on carbon cycling (Dias et al., 2020). At present, we are still largely unaware about how plants with alternative design (i.e. plants with a different suite of traits for coping under the same environmental



**FIGURE 3** Example of how combining the trait-based resilience approach can improve management of ecosystems. For instance, in salt marshes (grey) along an estuary sand content in the sediment varies along the estuary, being low at the head and higher at the mouth. Sand content reduces the marsh's capacity to resist erosion, thus marshes at mouth of the estuary will be more vulnerable to wave actions. However, if vegetation's root density is high, marshes' resistance to erosion will improve. Therefore, designing maps of marshes' sand content and root density will allow to determine which marsh is more vulnerable to erosion, that is, which marsh is less resilient and thus needs more active management

conditions) can influence ecosystem properties in ecosystems (Dias et al., 2020), particularly in coastal ecosystems, with implications for their resilience.

## 7 | CONCLUSION

Throughout this review, I have provided examples on how the application of a trait-based approach can highly increase our knowledge of ecosystem properties resilience. I have focused on coastal ecosystems here because first, these systems provide multiple important services for human population (e.g. coastal protection, carbon sequestration; Barbier et al., 2008; Nelson & Zavaleta, 2012) and, second, the forecast increases in coastal population (Neumann et al., 2015) and the threats posed by climate change (IPCC, 2019; Woodruff et al., 2013) will strongly impact on the capacity of these systems to deliver their services. Nevertheless, this resilience approach can be broadened to other ecosystems. For instance, in grasslands, studies have unravelled changes in plant traits under current climate change (e.g. Li, 2006). In turn, these changes in traits can alter the ecosystem properties, such as the water cycle or the pasture for livestock grazing (Garnier et al., 2016). Therefore, understanding how these changes translate into ecosystem property changes would allow to understand the ecosystem's resilience. Overall, a resilience framework based on traits and ecosystem properties can highly improve our understanding of how ecosystems change under current and future global changes.

## ACKNOWLEDGEMENTS

This work is based on PhD research and therefore I would like to thank my supervisor John N. Griffin for his precious advice and for helping in sharpening my ideas. I would like to thank John N. Griffin and Laurie Anne Myriam Wojcik for their comments on early drafts of this work that have highly improved the manuscript. I would also like to thank two anonymous reviewers for their helpful comments that allowed me to highly improve the manuscript. Furthermore, this work was supported by the Welsh Government and HEFCW through the 384 Sêr Cymru National Research Network for Low Carbon, Energy and Environment RESILCOAST Project.

## AUTHOR'S CONTRIBUTIONS

D.D.B. has conceived the idea and wrote the manuscript.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13641>.

## DATA AVAILABILITY STATEMENT

No data were generated for this work.

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**How to cite this article:** De Battisti D. The resilience of coastal ecosystems: A functional trait-based perspective. *J Ecol.* 2021;00:1–14. <https://doi.org/10.1111/1365-2745.13641>