

Differential effects of biological invasions on coastal blue carbon: A global review and meta-analysis

Ian C. Davidson¹ | Grace M. Cott^{1,2,3}  | John L. Devaney^{1,4} | Christina Simkanin¹

¹Smithsonian Environmental Research Center, Edgewater, Maryland

²School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland

³Environmental Research Institute, University College Cork, Cork, Ireland

⁴Botany Department, Trinity College Dublin, The University of Dublin, Dublin 2, Ireland

Correspondence

Grace M. Cott, School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland.
Email: g.cott@umail.ucc.ie

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Abstract

Human-caused shifts in carbon (C) cycling and biotic exchange are defining characteristics of the Anthropocene. In marine systems, saltmarsh, seagrass, and mangrove habitats—collectively known as “blue carbon” and coastal vegetated habitats (CVHs)—are a leading sequester of global C and increasingly impacted by exotic species invasions. There is growing interest in the effect of invasion by a diverse pool of exotic species on C storage and the implications for ecosystem-based management of these systems. In a global meta-analysis, we synthesized data from 104 papers that provided 345 comparisons of habitat-level response (plant and soil C storage) from paired invaded and uninvaded sites. We found an overall net effect of significantly higher C pools in invaded CVHs amounting to 40% ($\pm 16\%$) higher C storage than uninvaded habitat, but effects differed among types of invaders. Elevated C storage was driven by blue C-forming plant invaders (saltmarsh grasses, seagrasses, and mangrove trees) that intensify biomass per unit area, extend and elevate coastal wetlands, and convert coastal mudflats into C-rich vegetated habitat. Introduced animal and structurally distinct primary producers had significant negative effects on C pools, driven by herbivory, trampling, and native species displacement. The role of invasion manifested differently among habitat types, with significant C storage increases in saltmarshes, decreases in seagrass, and no significant effect in mangroves. There were also counter-directional effects by the same species in different systems or locations, which underscores the importance of combining data mining with analyses of mean effect sizes in meta-analyses. Our study provides a quantitative basis for understanding differential effects of invasion on blue C habitats and will inform conservation strategies that need to balance management decisions involving invasion, C storage, and a range of other marine biodiversity and habitat functions in these coastal systems.

KEYWORDS

biological invasion, blue carbon, carbon sequestration, coastal vegetated habitats, mangrove, saltmarsh, seagrass

1 | INTRODUCTION

Coastal wetlands play an important role in carbon (C) sequestration (Duarte, Losada, Hendriks, Mazarrasa, & Marbà, 2013; Mcleod et al.,

2011), but their precipitous loss over the last century endangers this critical function and other ecosystem services (Chmura, Anisfeld, Cahoon, & Lynch, 2003; Nellemann et al., 2009). Carbon

sequestered in coastal vegetated habitats (CVHs), specifically tidal marshes, seagrass beds, and mangrove forests, is termed “blue carbon” (Nellemann et al., 2009). A combination of high primary productivity, waterlogged conditions, and a distinctive efficiency for trapping suspended sediments enables long-term C storage by these ecosystems (possibly for millennia; Atwood et al., 2015; Fourqurean et al., 2012; Macreadie, Allen, Kelaher, Ralph, & Skilbeck, 2012; Nellemann et al., 2009). Degradation of blue C habitats reduces the potential for C sequestration and releases substantial stocks of previously sequestered C to the atmosphere (Pendleton et al., 2012). Pervasive eutrophication, siltation, mariculture, deforestation, land reclamation, and other land-use changes have led to widespread decline of blue C habitats (Figure 1) with estimated losses of up to 50% of global extent over the last century and current losses of ~8,000 km² annually (Alongi, 2002; Bridgman, Megonigal, Keller, Bliss, & Trettin, 2006; Duarte, Middelburg, & Caraco, 2005; Hamilton & Friess, 2018; Pendleton et al., 2012; Valiela, Bowen, & York, 2001). Consequently, advocacy for blue C conservation and restoration in international climate change agreements is gaining

momentum (Rogers, Macreadie, Kelleway, & Saintilan, 2018; Editorial, 2016; Herr, von Unger, Laffoley, & McGivern, 2017).

Concurrent with widespread losses of CVH, biological invasions have altered community composition of blue C habitats on a global scale (Zedler & Kercher, 2004), encompassing primary producers, herbivores, predators, and bioturbators; that is, a broad range of functional roles that mediate habitat stability and affect ecosystem services for which blue C habitats are renowned. Indeed, the invasion history of global blue C habitats is rich with complexity, and includes cryptic invasions at the haplotype level, intercontinental reciprocal invasions, and invasion-induced hybridization that have each produced major shifts in regional habitat composition and distribution (Daehler & Strong, 1997; Saltonstall, 2002). In several cases, CVH expansion at the scale of individual bays to regional coastlines has produced new invader-dominated habitats or converted mudflat to blue C habitat, including 112,000 ha expansion of introduced *Spartina* marshes along the coast of China, ~10,000 ha expansion of introduced seagrass in NE Pacific estuaries, and the completely novel introduction of mangrove habitat to oceanic islands (Figure 1; Supporting Information Table S1). Although these

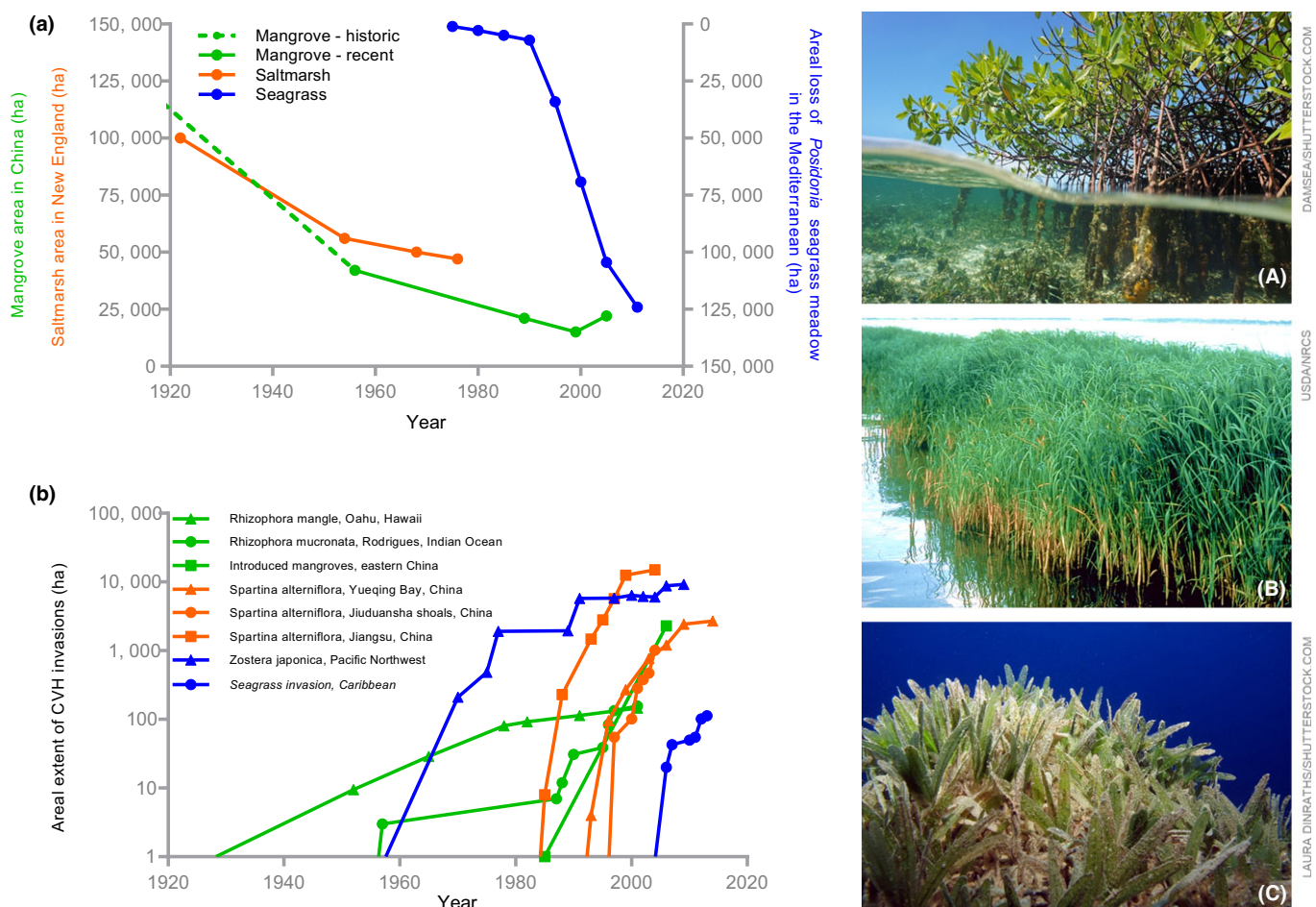


FIGURE 1 Decline and expansion of native and introduced blue carbon ecosystem engineers. Examples of (a) large-scale decline of blue carbon habitat and (b) mesoscale expansion of introduced habitat engineers, including *Rhizophora mangle* (A), *Spartina alterniflora* (B), and *Halophila stipulacea* (C). Data and sources for this figure are listed in Supporting Information Table S1 [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

expansions of coastal vegetated area are orders of magnitude smaller than losses of blue C habitat worldwide, habitat-forming plant invasions (i.e., ecosystem engineers) appear to be a primary countervailing cause of increasing CVH cover (along with CVH restoration, Wylie, Sutton-Grier, & Moore, 2016).

Understanding the effect of biological invasions on C cycling and storage is a pressing concern in a high CO₂ world in which C accounting, and promoting natural C sequestration, is prioritized (Herr, Pidgeon, & Laffoley, 2012; Pachauri et al., 2014). Much of the invasion-carbon research to date has focused on terrestrial ecosystems, following the pioneering work on habitat- and landscape-scale C flux in those systems (Dixon et al., 1994; Houghton, 2005; Peltzer, Allen, Lovett, Whitehead, & Wardle, 2010). A majority of work also focuses on introduced plants (Ehrenfeld, 2003; Liao et al., 2008; Vilà et al., 2011). Several studies have shown that C storage increases after invasion by plants, including in saltmarsh habitats, but the direction and magnitude of effects can vary, sometimes substantially, highlighting the role of context dependency of particular outcomes (Ehrenfeld, 2010; Vilà et al., 2011; Zedler & Kercher, 2004). Furthermore, a review of invasion effects on C in forest systems by Peltzer et al. (2010) provided critical context for the variety of responses that occur after introductions of species that span a full range of functional and trophic levels. Importantly, quantitative syntheses of invasion effects (both animals and plants) on C storage remain underreported, which undermines our ability to predict invasion outcomes and inform management actions. Such insights are especially urgent for CVHs in the face of rising sea levels and within a management context that requires balancing C storage with other ecosystem services and conservation goals that are also impacted by invasion.

In this study, we used a global meta-analysis to quantify the direction and magnitude of invasion effects on blue C pools for all introduced species for which data were available. We only considered biogeographical non-native species and not the spread of native species from neighboring habitats. This is the first such study focused exclusively on marine habitats. Specifically, we used published data from paired invaded and uninvaded areas of seagrass, saltmarsh, and mangrove systems to answer two main questions: (a) Do invaders alter C pools in CVH habitats? and (b) Do these effects differ by invader-type, including animals, structurally similar (blue C habitat forming) plants, and structurally distinct primary producers? We hypothesized that an overall increase in C storage would result from introduced plants, following earlier work in terrestrial systems and marshes (e.g. Liao et al., 2008), but predicted decreases in C storage due to animal invasions. We place our results in the context of ecosystem-based management and discuss the implications for C storage and sequestration in invaded blue carbon habitats.

2 | MATERIALS AND METHODS

2.1 | Data collection and eligibility criteria

We conducted a systematic review of peer-reviewed literature to examine the effect of introduced species on coastal blue C pools.

Three identical topic searches for each CVH type were conducted using the ISI Web of Science in December 2017, using the search terms: mangrove* AND (invasi* OR non-native OR nonnative OR non native OR exotic* OR non-indigenous OR non indigenous OR introduced); salt marsh* AND (invasi* OR non-native OR nonnative OR non native OR exotic* OR non-indigenous OR non indigenous OR introduced); and seagrass* AND (invasi* OR non-native OR non-native OR non native OR exotic* OR non-indigenous OR non indigenous OR introduced). The searches spanned published records from March 2, 1864, to November 30, 2017. The resulting papers were collated and screened to remove duplicate studies. Abstracts were then assessed against inclusion criteria (see PRISMA flow diagram in Supporting Information Figure S1), which were as follows: (a) relevant title and/or text and (b) experiments and/or observations conducted outdoors (not solely within a laboratory or greenhouse), on wild populations (not farmed or managed), and within a saltmarsh, mangrove, or seagrass habitat. Studies investigating saltmarsh, mangrove or seagrass invasion into unvegetated mudflat habitat (i.e., CVH expansion) were also included, but were analyzed separately. Full texts of the remaining articles were collated and examined for appropriate data. Each included study had to have a measure of C pools such as aboveground or belowground biomass, soil organic C, total soil carbon or soil organic matter in an invaded (treatment) and uninvaded (control) condition. Soil C pools were measured over a range of depths across studies. Within studies, however, comparisons of invaded and uninvaded depths and C pools were the same (i.e., directly comparable). If the published article did not include summary statistics of effects, like mean response, error, and sample size, authors were contacted directly to obtain missing information. If this was not possible, the study was excluded.

Our literature search provided 2,218 publications, and 492 remained after fulfilling title and abstract criteria (Supporting Information Figure S1). After detailed examination of full texts, 345 measures of effects were obtained from 104 published studies. Our raw dataset and list of publications used in analyses are available (Davidson, Cott, Devaney, & Simkanin, 2018). All but nine of the included papers were published after 1999, and the earliest study was published in 1984 (Supporting Information Figures S3 and S4). This may reflect a trend of recent increases in quantitative studies on biological invasions (Ricciardi & MacIsaac, 2008) and C pools in CVHs (Duarte et al., 2005). Studies with quantitative measures of effects were primarily from the northern hemisphere, with regional clusters on the west coast of North America, the east coast of North America, Western Europe, and the east coast of China (Supporting Information Figure S2).

2.2 | Data extraction and effect size calculation

For each study, we recorded the mean response, error, and sample size in invaded (treatment) and uninvaded (control) conditions, using Web Plot Digitizer to extract data from figures when necessary (Rohatgi, 2017). When a study reported a number of C pool responses for a single site, we limited data extraction to one

measure each of aboveground biomass, belowground biomass, and/or soil C pools per invaded–uninvaded paired comparisons to control for non-independence. If total biomass (e.g., whole plant) was reported in the absence of aboveground or belowground biomass, we used total biomass comparisons. If a paper included data from multiple sites, each site was considered as separate and independent data. If an article reported responses over time, the final time point was used in the analysis. If authors compared a non-invaded situation to situations of varying invader density, we used the most densely invaded scenario in the analysis.

The effect of introduced species on estimates of coastal blue C pools was measured for each experiment as the log-transformed response ratio,

$$\text{LnRR} = \ln\left(\frac{X_E}{X_C}\right)$$

where X_E is the mean response under the experimental condition and X_C is the mean response under the control condition (Koricheva, Gurevitch, & Mengersen, 2013). The LnRR represents the proportional change in measures of blue C pools in invaded habitats relative to uninvaded situations, irrespective of the original unit of measurement. In our study, positive LnRR values indicate a positive contribution (increase) of introduced species to coastal wetland blue C, and negative values are interpreted as negative effects on blue C, with zero values indicating no effect. To account for study precision, we calculated the variance of each effect size as,

$$v = \frac{(S_E)^2}{n_E X_E^2} + \frac{(S_C)^2}{n_C X_C^2},$$

where S is the standard deviation of treatment effect and n is the sample size. For before and after studies, variance calculations included a correlation coefficient, because data from these types of studies have a correlated-groups design, where individuals serve as their own control prior to treatment (as in Lajeunesse, 2011).

2.3 | Meta-analysis

We conducted a meta-analysis of the overall mean effects of non-native species on blue C pools in saltmarsh, mangrove, and seagrass habitats. A separate analysis was conducted to assess effects of a *non-native* saltmarsh, mangrove, or seagrass species invading or expanding into unvegetated mudflat habitats. Our methods and analyses followed rigorous protocols for the systematic review of literature and the development of statistically robust meta-analyses (see Supporting Information Table S2; Harrison, 2011; Koricheva & Gurevitch, 2014; Koricheva et al., 2013). All analyses were conducted with R software (R Core Team, 2016) using packages lme4 (Bates, Maechler, Bolker, & Walker, 2015), metafor (Viechtbauer, 2010), and picante (Kembel et al., 2010).

We assumed that heterogeneity was related to the variation in experimental design and species tested in our studies, and thus adopted a weighted random-effects model approach to testing main effects. In meta-analysis, a random-effects approach accounts

for additional between-study variance by calculating study weight (w_k) as,

$$w_k = \frac{1}{v_k + \sigma^2},$$

where v_k is the effect size variance and σ^2 is the between-study variance parameter (Koricheva et al., 2013).

We tested the overall effect size of introduced species on blue C pools in CVH, as well as separately testing effects of a priori selected groups, namely habitat-type (mangrove, saltmarsh, seagrass), C pool (aboveground biomass, belowground biomass, soil C), and invader-type. We used three categories of invader-type: structurally similar primary producer (i.e., an introduced mangrove, saltmarsh, or seagrass species invading a similar habitat, such as an invasive mangrove tree in a native mangrove forest); structurally distinct primary producer (i.e., an invasive plant or algae which is not foundational to the habitat being invaded, such as a seaweed invading a seagrass habitat); and animals (mammals and invertebrates). To test the statistical significance of overall effects and each grouping, we constructed 95% confidence intervals around our weighted mean of studies, following Koricheva et al. (2013). Mean effect sizes were considered significant ($\alpha = 0.05$) when 95% confidence intervals did not overlap with zero.

As an additional step in our analysis, we explored sources of variation in effect sizes among a series of explanatory variables. For example, we were interested in whether the effect of introduced species differed between blue C habitats, invader-type, and C pools. To test our hypotheses, we performed linear mixed-effects models using (a) our full dataset of effect sizes as the response, (b) habitat-type, C pool, and invader-type as fixed predictor variables, and with (c) study included as a random factor. We ran mixed models with variance weighted and unweighted effect sizes and found no significant differences; therefore, results for the variance weighted effect size models are presented. For all mixed models, significance of each variable was tested using likelihood-ratio tests of reduced versus full models. To assess effects of introduced species on expansion of blue C pools, we repeated the above analysis using published results where a blue C foundation species (mangrove, saltmarsh, or seagrass species) was introduced to an unvegetated (mudflat) habitat. We again tested overall effects of introduced species on blue C in terms of habitat-type (mangrove, saltmarsh, seagrass) and C pool recorded (aboveground biomass, belowground biomass, soil C).

2.4 | Sensitivity analysis

To ensure robust interpretation of our results, we performed several analyses to determine the sensitivity of our meta-analysis, following the methodological criteria recommended by Koricheva & Gurevitch (2014) and Koricheva et al. (2013). First, we re-tested overall effects and mixed models using an unweighted approach. We examined the robustness of our results by determining the relative contribution of studies with particularly large effect sizes. To

do this, we ranked data points by magnitude of effect, systematically removed the largest magnitude data point (regardless of direction of the effect) in stepwise order, and repeated the meta-analysis to determine how many removed data points were required to change the significance of results. To quantify the extent of methodological heterogeneity between studies and its impact on effect sizes, we calculated the I^2 statistic (Higgins & Thompson, 2002) for our complete dataset. The I^2 statistic quantifies the amount of heterogeneity in the dataset. As the I^2 value approaches 0%, variation in effect size is more attributable to random error whereas the closer it is to 100%, effect size variability can be interpreted as being related to some predictor variables, which may be elucidated by subgroups analysis.

The magnitude of effect sizes may change over time due to changes in methodological and analytical techniques. Because our analysis included data published between 1984 and 2017, we tested for temporal changes in responses by including year of publication as a moderator in our mixed models. The phylogenetic histories of species compared in ecological meta-analysis can also influence effect sizes, as closely related species often display similar traits that can lead to similar estimates of effects, violating assumptions of independence. We tested the influence of phylogenetic relatedness on effect sizes in pairwise comparisons of higher plants (including mangrove, saltmarsh, and seagrass species). This analysis was limited to higher plants because phylogenetic relationships have been enumerated for this group. Relatedness was determined using the Web-based program Phylomatic (Webb & Donoghue, 2005) and a phylogenetic tree and relatedness matrix was produced using the R package “picante” (Kembel et al., 2010).

We checked our dataset for publication bias (i.e., underreporting of studies/observations showing no effects) using (a) visual assessments of contour enhanced funnel plots; (b) correlation (Spearman's ρ) tests between effect sizes and variances; and (c) calculations of Rosenthal's fail-safe number (i.e., the number of additional “negative” studies that are needed to increase the p value above 0.05). Bias was examined within datasets used for analysis of invasions into CVH, introduced foundational species invasions into unvegetated habitats, and all effects combined.

3 | RESULTS

3.1 | Differential effects of invasion on blue C storage

The global synthesis revealed a significant net enhancement of C storage per unit area in invaded CVH compared to adjacent unvegetated areas (mean $ES = 0.34$, 95% CI 0.19–0.49; Figure 2). This reflects the published research on the effect of 34 non-native species (including hybrid and subspecies) on coastal blue C pools worldwide (Supporting Information Table S3). Invaders included a range of species, such as non-native marsh plants, mangrove trees, seagrasses, macroalgae, terrestrial herbivores, marine grazers, and epibiont species. The overall effect of 40% higher C storage (Table 1) was driven

by invasions of plant species that are structurally (and taxonomically) similar to the foundational (engineering) plants of the recipient habitat, wherein marsh grasses invaded saltmarshes, seagrass species invaded seagrass beds, and mangrove tree species invaded mangroves. These structurally similar species were the prevailing invader-type in the dataset (72%) relative to structurally distinct primary producers (12%) and animals (16%). Their incursions were associated with an average 117% increase in C storage compared to uninvaded habitat (Table 1). Significant C-enhancement in invaded habitat was recorded for aboveground biomass, total (plant) biomass, and soil C, but there was no significant effect on belowground biomass (Figure 2). The magnitude of effect did not differ among these C pools (Supporting Information Table S4; $\chi^2 (2) = 5.150$, $p = 0.076$).

Introduced animal and structurally distinct primary producers had significant negative effects on C storage (Figure 2). Structurally distinct primary producers included algal invaders of seagrass beds, marsh grass invasions of mangroves, and tree invasions of saltmarshes, which caused consistent and significant declines in habitat biomass (overall average -37% , Table 1) through species displacement, epibiosis, and overtopping. Similarly, animal invasions of blue C habitats that resulted in herbivory, predation, trampling, bioturbation, and epibiosis led to a significant net reduction in C storage relative to uninvaded habitat (overall average -47% ; Table 1; mean $ES = -0.65$, 95% CI -0.41 to -0.89 ; Figure 2).

The effect of invasion differed among habitat-types (Figure 2). Introduced species enhanced C pools in saltmarshes (mean $ES = 0.65$, 95% CI 0.47–0.84), there was a significant reduction in C storage in seagrass habitats (mean $ES = -0.50$, 95% CI -0.79 to -0.21), and there was no significant effect of invasion on mangrove C storage (Figure 2). Mixed models revealed no differences across habitat-types, however (Supporting Information Table S4; $\chi^2 (2) = 0.663$, $p = 0.718$), primarily because effect sizes were driven by invader-type rather than recipient habitat (Supporting Information Table S4; $\chi^2 (2) = 19.36$, $p < 0.001$). Although invader-type was distributed unevenly per habitat, the direction of invader-type effects was largely consistent. For example, animal invasions had negative effects on C storage in both saltmarshes and seagrass beds. No studies of animal invasions of mangrove forests were captured in this review, presumably because habitat-level effects of such invasions, to the extent that they occur, have yet to be broadly explored. By contrast, animal and algae invasion, which had consistent negative effects on plant-based C pools across habitats, comprised the majority of comparisons (83%) for seagrass habitats.

3.2 | CVH expansion into unvegetated habitat

The effect of mudflat conversion to blue C habitat by non-native species was striking for C storage (Figure 3), linked to obvious structural differences between unvegetated and plant-dominated habitats. Expansion of habitat-forming plant invaders into unvegetated mudflats significantly increased C pools (mean $ES = 1.45$, 95% CI 0.94–1.96, Figure 3). The mean aboveground biomass effect size for mudflat invasions was five times higher than mean soil C storage effects

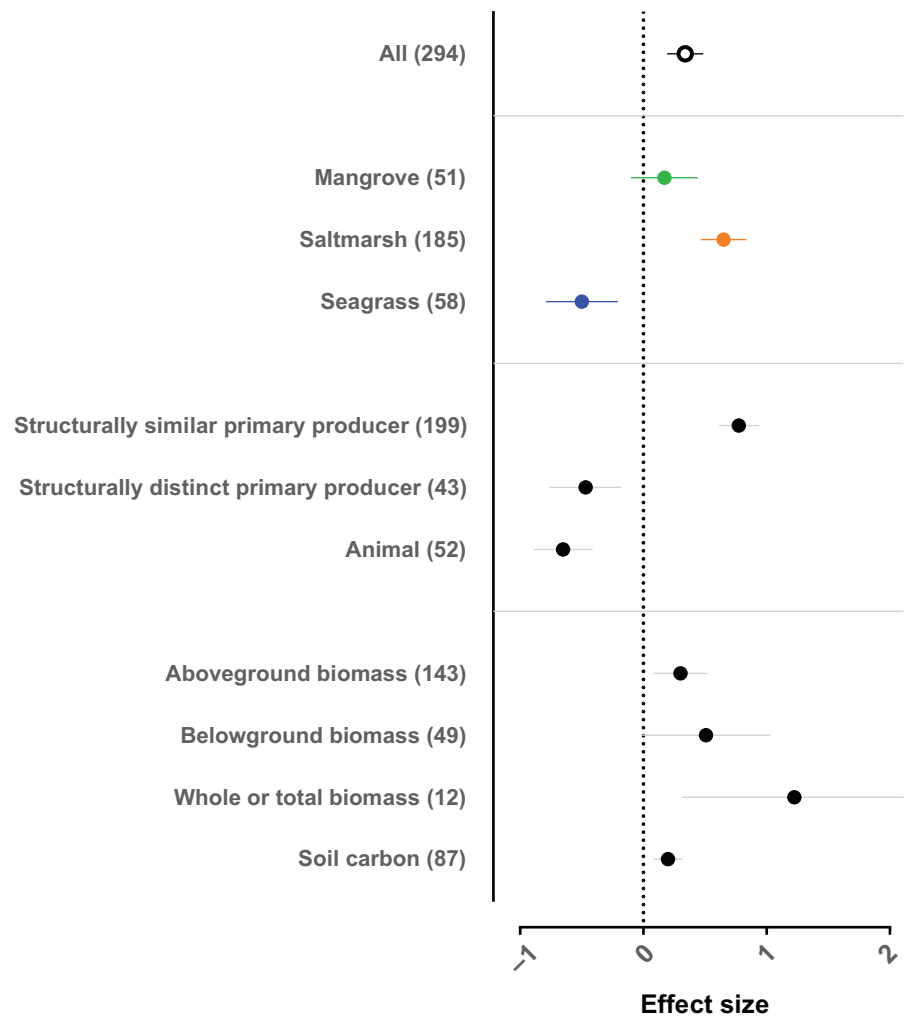


FIGURE 2 Effects of species invasions on C pools in coastal vegetated habitats ($n = 294$). The x-axis is the log response ratio of C pools in invaded vs. non-invaded areas, grouped by habitat-type, invader-type, and C pool. Positive values indicate larger C pools in invaded conditions, negative values indicate larger C pools in uninvaded conditions, and zero values indicate no differences [Colour figure can be viewed at wileyonlinelibrary.com]

(Supporting Information Table S4; $\chi^2 (2) = 14.38, p < 0.001$). Soil C was sampled more often, however, and the overall effect of CVH expansion was an increase of $158\% \pm 29\%$ (Table 1). Only two of 51 comparisons measured C storage effects of non-native seagrass expansion into mudflats with no differences in invaded versus uninvaded soil C pools (Larned, 2003).

3.3 | Sensitivity analysis

No changes were recorded when overall effects and mixed models were re-tested using an unweighted approach. Sensitivity analysis revealed that mean effect sizes and heterogeneity statistics were robust across all response variables (habitat-type, invader-type, and C pool) and results were not driven by individual large effects or outliers. A stepwise process to systematically remove the largest magnitude data point (regardless of effect direction) resulted in a range from 13% of effects (for soil C) to 96% of effects (for animal invaders and belowground biomass) being removed before mean effects changed in significance. Similarly, sensitivity analysis showed that results were robust for assessments of CVH invasions of unvegetated mudflat across all response variables (invader-type and C pool).

There were high levels of heterogeneity in the dataset of invasions into CVH ($I^2 = 99\%, p < 0.001$) and expansion of non-native CVH species into unvegetated mudflat habitats ($I^2 = 99\%, p < 0.001$). This indicates that variance recorded in our meta-analyses was not primarily explained by sampling error, but instead by predictor variables like invader-type. We found no significant effect of publication year in our meta-analysis for invasions into blue C habitats (Supporting Information Figure S3; $\chi^2 (1) = 0.09, p = 0.77$) or CVH species invasions into unvegetated mudflat habitats (Supporting Information Figure S4; $\chi^2 (1) = 0.166, p = 0.68$). A phylogenetic signal in effect size was analyzed using a mixed-modeling approach. For our subset of studies of higher plant invasions into CVH, the phylogenetic relatedness of invasive and native species was not significant (Supporting Information Figure S5; $\chi^2 (1) = 0.0155, p = 0.9$).

Contour enhanced funnel plots and Spearman's correlation tests showed no publication bias in our dataset of invasions into CVH ($\rho = -0.005, p = 0.931$) and all studies combined ($\rho = 0.006, p = 0.913$; Supporting Information Figure S6). There was a significant correlation between effect size and sampling variance in the dataset of CVH invasions of unvegetated mudflat (i.e., high asymmetry; $\rho = 0.341, p = 0.013$). This was driven by the true effects of C pool

TABLE 1 Percentage change in C pools across habitat-types, invader-types, and C pool in response to biological invasion. Percentage of change is represented as the mean \pm 95% confidence intervals

Variable	Percentage change ($e^{\mu}-1$) \times 100%	n
Invasions into coastal vegetated habitats		
Habitat-type		
All	40.55 \pm 15.81	294
Mangrove	18.61 \pm 31.27	51
Saltmarsh	91.73 \pm 20.25	185
Seagrass	-39.25 \pm 33.67	58
Invader-type		
Structurally similar plant	117.04 \pm 17.87	199
Structurally distinct plant	-37.38 \pm 33.78	43
Animal	-47.83 \pm 27.12	52
Carbon pool		
Aboveground biomass	35.09 \pm 24.51	143
Belowground biomass	66.31 \pm 68.51	49
Total biomass	240.89 \pm 148.18	12
Soil carbon	22.09 \pm 12.72	87
Mangrove, saltmarsh, seagrass invasions into mudflats		
Invader-type		
All	326.70 \pm 66.46	51
Mangrove	96.05 \pm 19.79	7
Saltmarsh	419.55 \pm 82.47	42
Seagrass	-6.27 \pm 56.31	2
Carbon pool		
Aboveground	7254.52 \pm 2450.31	6
Belowground	672.92 \pm 39.32	5
Soil carbon	158.31 \pm 29.46	40

Note. Significant effects are in bold.

increases on mudflats that are invaded by a blue C species (i.e., non-native saltmarsh, mangrove, or seagrass) rather than publication bias, however. Rosenthal's fail-safe numbers—157737 (invaders in blue C habitats), 132792 (blue C invaders in unvegetated mudflat habitats), and 580311 (all data)—were much greater than the minimum appropriate fail safe for each of the three datasets (calculated as $5k + 10$, where k is the number of effects in the meta-analysis; Rosenthal, 1979).

4 | DISCUSSION

4.1 | Differential effects of invasion on blue C storage

This review and synthesis provides quantitative support for conceptual frameworks on differential effects of invasion on C storage in ecosystems (Peltzer et al., 2010) and is one of the first such

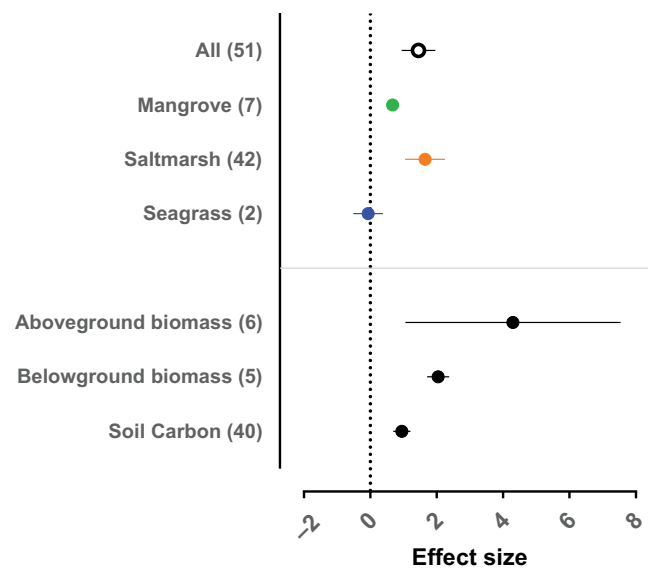


FIGURE 3 Effects of blue C invaders (mangrove, saltmarsh, seagrass species) on C pools in unvegetated coastal habitats ($n = 53$). The x-axis is the log response ratio of C pools in invaded vs. non-invaded areas, grouped by habitat-type and C pool. Positive values indicate larger C pools in invaded conditions, negative values indicate larger C pools in uninvaded conditions, and zero values indicate no differences [Colour figure can be viewed at wileyonlinelibrary.com]

syntheses for marine systems. The overall increase in blue C reported here was driven by habitat-forming plant invaders (saltmarsh grasses, mangrove trees, and seagrasses) that intensify biomass per unit area, extend and elevate coastal wetlands, and convert coastal mudflats into C-rich vegetated habitat. These plant invaders increased C storage by producing larger plants, higher density, deeper and larger root systems, or more efficient sediment entrapment compared to uninvaded areas—many of the traits of higher resource acquisition and resource-use efficiency that are typically associated with plant “invasiveness” in these habitats (Liao et al., 2008). By contrast, the net effect of animal invasions was a reduction ($-48\% \pm 27\%$) in blue C pools, largely caused by herbivory, trampling, and borrowing that removed vegetation or destabilized habitat (Bertness, 1984; Davidson & De Rivera, 2010; Sharp & Angelini, 2016). Similarly, a significant reduction in C storage ($-37\% \pm 34\%$) resulted from structurally distinct primary producer invasions, mainly triggered by displacement or reduced density of native seagrasses by seaweeds and mangroves by marsh grasses (Ceccherelli & Campo, 2002; Drouin, McKindsey, & Johnson, 2012; Feng, Ning, Zhu, & Lin, 2017; Zhang, Huang, Wang, Chen, & Lin, 2012). These effect directions and sizes improve our understanding of C storage response to invasion in marine systems and provide further insight and some alignment with similar examinations of plant and animal invasion on C pools in terrestrial systems (Liao et al., 2008; Qiu, 2015).

While the mean effect of each invader-type underpinned the overall effects measured in this meta-analysis, the effect of each species within invader categories was not directionally uniform. Within-group variation was recorded, sometimes with the same

species contributing to increased *and* decreased C storage at different sites. This provides some additional support for context dependency of invader effects on ecosystems (Hulme et al., 2013; Vilà et al., 2011). The overall effect of invasion by structurally similar primary producers—more than a doubling of the C pool compared to uninvaded habitat ($117\% \pm 18\%$)—was determined from 199 comparisons in which 80% had higher C storage in the invaded scenario. There were several introduced species that affected higher *and* lower C storage compared to native habitat within the same regions, including the marsh grass *Phragmites australis* on the U.S. Atlantic Coast, the marsh grass *Spartina alterniflora* and mangrove *Sonnerata apelata* in China, and the introduced seagrass *Zostera japonica* in U.S. Pacific estuaries (Davidson et al., 2018). Possible reasons for counter-directional C responses to the same species are the magnitude of difference between invader traits and recipient (native) community traits (Martin, Newton, & Bullock, 2017) or differences in duration since establishment of the invader (Strayer, Eviner, Jeschke, & Pace, 2006). While we did not measure traits of native versus invader species, we found no signal that recipient community composition differed between cases where a particular invader increased and decreased C storage. Moreover, we categorized primary producers by how similar and different they were to the system they invaded and found significant impacts on C storage in opposite directions. We could not obtain site-specific data on the length of time an invader was established and further research on C response throughout the invasion process in CVHs would be beneficial, especially if C balance switching occurs as invasions progress, as has been documented in forests (Peltzer et al., 2010).

This study's inclusion of animal invasion effects on C storage is relatively uncommon in a literature more focused on (terrestrial) plants and bottom-up processes in C pools (Atwood et al., 2015; Pyšek et al., 2012; Vilà et al., 2011). Introduced animals had significant negative effects on C storage, driven by non-native herbivorous mammals, mollusks, and crustaceans, but there were instances whereby predators enhanced habitat biomass (Bertness & Coverdale, 2013). Indeed, as recorded for invasions by structurally similar primary producers, differential effects of animal invasion included an example for the *same* species in different systems or locations. The invasive green crab, *Carcinus maenas*, is playing a role in the recovery of New England salt marshes by exerting previously depleted top-down control on a native herbivore, a finding that supports a positive effect of invasive animals in promoting CVH regrowth and blue C storage outside their native ranges (Coverdale et al., 2013). This example is one of the few cases of indirect effects on C storage in our dataset. Atwood et al. (2015) similarly highlighted the importance of predators—typically species within their native ranges—in protecting C stocks. *C. maenas* is also associated with major losses of seagrass habitat in northern New England and Atlantic Canada, where major declines of meadows are linked to green crab digging for prey, burrowing for shelter, and direct cutting of plant material (Matheson et al., 2016; Neckles, 2015). Therefore, while the mean effect of animal invasion was to significantly reduce C storage in CVHs, it is important to mine data comparisons within overall effects

from meta-analyses, especially in cases where management actions are being considered (Hulme et al., 2013; Pyšek et al., 2012; Qiu, 2015).

Whereas invasion by structurally similar primary producers was reported most often for saltmarshes in our dataset, just one of 43 comparisons for structurally distinct primary producer invasion occurred in a saltmarsh. In that case, saltmarsh biomass in Florida was reduced an order of magnitude (at local spatial scales) by overtopping incursion from landward stands of the introduced Brazilian Pepper tree (*Schinus terebinthifolius*) (Spector & Putz, 2006). A majority of comparisons (88%) involving structurally distinct primary producers resulted in lower CVH C storage compared to uninvaded habitats, mainly because of displacement of CVH species by introduced plants and algae, but also from the possible decline of CVH species which opened space for invasion. In either scenario, loss of CVH species occurs without replacement by native or invading species that reengineer the same habitat, causing apparent reductions in the C pool. In seagrass systems, a range of algal invaded sites—by *Caulerpa taxifolia*, *Caulerpa racemosa*, *Codium fragile*, *Gracilaria vermiculophylla*, *Lophocladia lallemandii*—were found to have reduced biomass or C storage compared to uninvaded meadows (Ballesteros, Cebrian, & Alcoverro, 2007; Ceccherelli & Campo, 2002; Drouin et al., 2012; Thomsen, Stæhr, Nejrup, & Schiel, 2013; Williams & Grosholz, 2002). Likewise, the rich C pool that occurs in Chinese mangrove systems is being reduced by incursions of invasive *Spartina alterniflora* (Feng et al., 2017; Zhang et al., 2012). The reverse of this phenomenon—mangrove incursion into saltmarsh environments—is also occurring within adjacent native systems (Saintilan & Williams, 1999), but was not captured in this study because we only considered biogeographical non-native species and not the spread of native species from neighboring habitats.

While our findings of differential mean effect sizes and directions were robust, these results are reflective of locations, habitats, and taxonomic groups studied (and published) on invasion and C pools in CVH systems. As such, meta-analyses synthesize what has been studied and employ sensitivity analyses to explore sources of potential bias (Gurevitch, Koricheva, Nakagawa, & Stewart, 2018), but are constrained by absences of data that could further elucidate what is happening in nature (Gurevitch & Hedges, 1999). The relative disparity of comparisons among habitat-types reflects understudied invasion impacts (and C dynamics) in seagrass and mangrove systems compared to saltmarshes. The effects of 34 introduced species in total are reported in this study, but the range of CVH-invading species is much broader. For example, Williams (2007) reported 60 species introductions in seagrass meadows or by seagrass species worldwide, but relatively few studies have captured any impact data for these species, much less their effects on C storage. Similarly, studies of animal invasions and their impact on (plant-based) C pools in CVHs are under-represented. There were examples of introduced animal impacts (e.g., wild horse trampling and deer grazing) that reduce biomass or habitat extent but did not fit the inclusion criteria for this study (e.g., for lack of an uninvaded area

comparator). Other recent and remarkable examples, such as the decline of saltmarsh biomass and habitat affected by an introduced insect (*Nipponaclerda biwakoensis*) in the Mississippi Delta, have been reported in the popular media (Baurick, 2018) but were not in the scientific literature until very recently (outside the scope of this analysis; Knight et al., 2018). Further research could also expand on understudied regions and spatial scale of invader influence on blue C worldwide and, crucially, include longer term measures that better capture the consequences for sequestration and longer term C pool stability.

4.2 | Blue-C habitat extent in a highly invaded world

Ideally, our evaluation of invasion effects on CVH C pool responses would have included data on habitat extent, expressed as loss or expansion of CVH areal cover over time. We were able to address aspects of this issue by (a) reconstructing invasion-based CVH expansion using the few detailed studies that provided invasion histories linked to explicit estimates of habitat area over time (Figure 1); (b) capturing a handful of studies in the structured meta-analysis that reported habitat loss in invaded and uninvaded areas at a local level; and (c) through comparisons of blue C consequences from introduced CVH species' conversion of mudflats. Expansions of introduced CVH, often intentionally introduced, have promoted remarkable development of blue C habitat at the estuary or bay scale in some regions (Liu, Zhou, Qin, & Zhou, 2007; Ren et al., 2009) and include biogenic habitat with no native analogue in some systems (Allen, 1998). Because these expansions are often linked to conversion of mudflat habitat, they result in new pools of above- and belowground biomass and significantly higher levels of soil C (Figure 3), although other biodiversity and habitat functions can also be affected.

More broadly, however, larger scale regional or landscape-level data on invasion-related CVH extent was not forthcoming. This hinders our ability to multiply (scale-up) robust data on invasion effects per unit area. As a result, estimates of CVH C pools, expansion and degradation at regional and continental scales are bounded by high levels of variation and uncertainty, largely driven by limited baseline information on CVH extent and an over-reliance on a few early coarse estimates of broad-scale CVH cover (Bridgman et al., 2006; Bromberg & Bertness, 2005; Pendleton et al., 2012). Historical reconstructions of changes to CVH, which are especially important to understand the temporal trend of CVH loss over time, have proven difficult because of questionable reliability of older historical data (especially subtidal) or mismatched comparisons (Boudouresque, Bernard, Pergent, Shili, & Verlaque, 2009; Leriche, Boudouresque, Bernard, Bonhomme, & Denis, 2004; Mattson, Frazer, Hale, Blich, & Ahijevych, 2007; Waycott et al., 2009).

Prospects for more accurate CVH mapping in the future have improved dramatically, however, because of methodological improvements underpinned by modern remote sensing, underwater mapping techniques including side-scan sonar, and modeling and

analyses of big data (Boudouresque et al., 2009; Bridgman et al., 2006; Marvin et al., 2016). Efforts to account for CVH habitat extent and carbon storage, even with high levels of uncertainty, are very valuable in an era of rapid climate change (Holmquist et al., 2018), and especially for environmental carbon accounting and determining carbon balances across a range of perturbations (Bridgman et al., 2006). Recent research combining large sample sizes over broad geographic ranges provides improved estimates of coastal wetland carbon balances (Tollefson, 2018). Research on carbon flux and sequestration is rapidly evolving as our understanding of climate change dynamics and habitat responses grows (Arias-Ortiz et al., 2018; Barnes, 2017; Howard et al., 2017) and the role of CVH and their invasions is an important component for predicting future trends.

4.3 | Ecosystem-based management and balancing conservation goals

Human-caused shifts in C cycling and biotic exchange are defining characteristics of the Anthropocene (Ehrenfeld, 2010; Lewis & Maslin, 2015). As a result, C mitigation and invasion feature prominently in international environmental policy (United Nations Environment Programme, 1992; United Nations General Assembly, 1994), in which blue C habitat degradation, conservation, and restoration have recently come to the fore (Herr et al., 2012; Macreadie et al., 2017). Our analysis shows that invasions by structurally similar primary producers broadly enhance C storage compared to uninvaded sites and are recognized for traits that promote habitat stability (Fei, Phillips, & Shouse, 2014). In some contexts, plant invasions are lauded for their potential to accrete shoreline habitat (e.g., marsh and mangrove soil) at a higher rate than sea-level rise, providing a valuable counterpoint to coastal erosion and enhancing prospects for long-term C sequestration (Caplan, Hager, Megonigal, & Mozdzer, 2015). These same invasion features and services are also a cause for concern, however, because they can alter hydrology and reduce runoff flow rates, displace native plants, alter physical habitat structure, shift trophic structure, impact bivalve fisheries, and convert foraging habitat affecting resident and migratory birds (Chimmer, Fry, Kaneshiro, & Cormier, 2006; Grosholz, Levin, Tyler, & Neira, 2009; Zedler & Kercher, 2004). Such effects have prompted management actions to restore systems to their pre-invasion state (Hedge, Kriwoken, & Patten, 2003; Lampert, Hastings, Grosholz, Jardine, & Sanchirico, 2014). In fact, control and eradication of invasive species in CVHs are implemented in several contexts (Creese, Davis, & Glasby, 2004; Shafer, Kaldy, & Gaeckle, 2014) and are promoted under the Convention on Biological Diversity (United Nations Environment Programme, 1992). The juxtaposition of C and other function conservation is striking: For example, Grosholz et al. (2009) described and predicted U.S. West Coast geomorphic impacts of *Spartina* invasion as (a) increasing sediment accumulation and stability, (b) increasing organic matter accumulation, (c) raising habitat elevation, (d) increasing litter buildup, and (e) altering belowground geochemical

conditions (via root-mediated flux, plant litter build up, and degradation), each contributing to direct and indirect negative impacts on native community structure and function that are of conservation value. Yet these exact conditions are also considered valuable ecosystem services in blue carbon research and conservation focused on climate mitigation.

Resolving conflicting ecosystem management goals is a widely recognized challenge. Recent studies of habitat multifunctionality suggest novel habitat-engineering invasions could be viewed as beneficial additions to coastal ecosystems (Ramus, Silliman, Thomsen, & Long, 2017), although the services provided by uninvaded habitat have been underestimated in some accounts, including the range of functions performed by mudflats (including C storage, Bridgman et al., 2006). Persuasive examples of CVH restoration to remove invasive species showcase approaches that ensure continuation of desired habitat functions during restoration by phasing management actions to prevent lapses in ecosystem services (Lampert et al., 2014; Valiela & Fox, 2008). Our results indicate that subsets of CVH invaders (i.e., structurally distinct primary producers and animals in most contexts) provide a straightforward management goal of removal or control because they threaten C storage, habitat stability, and biodiversity (Macreadie et al., 2017). Such approaches may require restoration of depleted native populations in cases where introduced species appear to be fulfilling a vacated role, as in the case of introduced green crab in New England saltmarshes (above). However, a more challenging management process is likely for many non-native CVH ecosystem engineers, which buttress proposed blue-C management goals in existing frameworks (United Nations Framework Convention on Climate Change: resolution/adopted by the General Assembly, 20 January A/RES/48/189 C.F.R., 1994), but fundamentally alter other conditions of conservation value that are also embedded in regional, national, and international conservation policy (Genovesi, Carboneras, Vilà, & Walton, 2014; United Nations Environment Programme, 1992; United States Congress, 1996). The tension between management goals is urgent because the magnitude and extent of invasion continue to grow at a time when the value of C-related ecosystem services is increasingly recognized. Should managers accept some of the costs imposed by blue-C enhancing invaders, or can stable C storage be achieved in CVHs while removing exotic species and restoring native habitat composition and functioning? It is incumbent on researchers, stakeholders, and policymakers to tackle this conflict head-on and develop strategies and recommendations for managing invasive species and blue carbon within these habitats in ways that reduce the management impact of one on the other.

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DATA ACCESSIBILITY

Data accessible via figshare repository (Davidson et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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