



Early invasion of common cordgrass (*Spartina anglica*) increases belowground biomass and decreases macrofaunal density and diversity in a tidal flat marsh

Wonhyeop Shin · Minwoo Oh · Jae-Sang Hong ·
Chaeho Byun · Eun Ju Lee

Received: 6 June 2021 / Accepted: 28 June 2022
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Abstract *Spartina anglica* (hereafter *Spartina*) is an invasive perennial marsh grass shifting hydrodynamic regime and sediment characteristics in invaded area, thereby reducing macrobenthic diversity. There have been only a few studies focusing on the patch structure of *Spartina* according to size and its effects on macrofauna. A field experiment was conducted to identify

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10530-022-02866-8>.

W. Shin · M. Oh · E. Lee (✉)
School of Biological Sciences, Seoul National University,
Seoul 08826, Republic of Korea
e-mail: ejlee@snu.ac.kr

W. Shin
Interdisciplinary Program in Landscape Architecture,
Seoul National University, Seoul 08826, Republic of Korea

W. Shin
Transdisciplinary Program in Smart City Global
Convergence, Seoul National University, Seoul 08826,
Republic of Korea

J.-S. Hong
Department of Ocean Sciences, Inha University,
Incheon 22212, Republic of Korea

J.-S. Hong
Korea Institute of Coastal Ecology, Bucheon 14449,
Republic of Korea

C. Byun
Department of Biological Sciences and Biotechnology,
Andong National University, Andong 36729,
Republic of Korea

effects of *Spartina* patches where they have been introduced no later than 5 years after invasion occurred on macrofauna assemblages in Ganghwa Island, South Korea. The survey area was divided into two sections according to vegetation: (1) *Suaeda japonica* vegetation from 0 to 60 m away from the levee, and (2) bare mudflat from 60 to 90 m away from the levee. The patch sizes of *Spartina* were categorized into small (1–4 m²), medium (5–11 m²), and large (13–40 m²) in area with four replicates for each section. The biomass ratio of the belowground and aboveground in the small size patch of *Spartina* was significantly higher than those in the medium and large size patch of *Spartina*. It indicated that more resource was allocated to rhizomes in small size patch with short invasion history (1–2 years). After *Spartina* invaded, macrofauna richness (70%), Shannon–Wiener diversity (80%), and density (67%) were decreased. However, infaunal deposit-feeding polychaete *Perinereis lineata* and epifaunal gastropods *Batillaria cumingi* and *Lactiforis takii* increased by *Spartina*. Ordination of macroinvertebrate assemblages separated the habitat with *Spartina* invasion from the adjacent uninvaded tidal flat and *Suaeda japonica* habitats. This study offers a significant insight into early invasion strategies of an aggressive plant invader, *Spartina* for management of coastal wetlands and its impacts on macrofaunal assemblages.

Keywords Biomass allocation · Macrobenthos communities · Patch size · *Spartina* · Species diversity · Tidal flat marsh

Introduction

Tidal flats and salt marshes provide diverse ecosystem services, as well as food and habitat to numerous animal fauna such as benthic macrofauna, birds, and fish (Costanza et al. 1997; Barbier et al. 2011). Mudflats form an integral part of estuarine coastlines and play an important role in flood defense (Möller et al. 2014). Mudflats also act as an essential sediment source for adjacent salt marshes (Temmerman et al. 2004; Ganju et al. 2015). However, ecosystem destruction and alien species invasion are increasing due to anthropogenic disturbance and global climate change (Worm et al. 2006; Ayres and Strong 2002). Wetlands and coastal habitats are particularly vulnerable to invasive species due to the influence of tidal dynamics and frequent disturbances (Lodge 1993; Boorman 1999; Schirmel et al. 2016).

The grass *Spartina anglica* CE Hubbard (Poaceae) was first discovered on Ganghwa Island in Incheon, South Korea in 2008 (Raybould et al. 1991; Hedge et al. 2003; Kim et al. 2019); it was designated as one of the world's worst invasive alien species by the International Union for Conservation of Nature (IUCN) in 2000, and as a harmful marine organism by the South Korean Ministry of Ocean and Fisheries in 2016. *Spartina anglica* is thought to have evolved following hybridization between *Spartina alterniflora* Louiseleur from the northeastern United States with *Spartina maritima* Fernald, a native species of the southern coast of England (Raybould et al. 1991; Baumel et al. 2002). Hereafter, we will call *Spartina anglica* as *Spartina* because *Spartina anglica*, *Spartina alterniflora*, and *Spartina maritima* are all belong to *Spartina* genus and their distinction is still under further investigation. Various *Spartina* species have been deliberately introduced in estuarine and coastal habitats of Britain (Gray et al. 1991), North America (Ayres and Strong 2002), China (Chung 1993; Zuo et al. 2012), Japan (Kimura et al. 2016), New Zealand (Hubbard and Partridge 1981), and Australia (Kriwoken and Hedge 2000) to stabilize tidal flats, levees, and coastlines.

The development and propagation of *Spartina* strains is still ongoing, destroying existing native vegetation and changing ecological environments worldwide (Cutajar et al. 2012; Daehler et al. 1996; Xiao et al. 2010). *Spartina* transforms marine habitats into monocultures (Hacker et al. 2001), changes sediment

characteristics such as grain size, pH, salinity, and organic matter content (Hubbard and Stebbings 1968; Netto and Lana 1997; Sheehan and Ellison 2014), and retards the flow of water through stiff aboveground shoots (Morris et al. 2002; Bouma et al. 2010; Quan et al. 2016). Several studies have examined the influence of *Spartina* on macrofauna; it has been reported to block energy supply to tidal flat macroalgae as its shoots reduce light transmittance, thereby significantly altering macrobenthic communities and the food web (Netto and Lana 1997, Thompson 1991; Levin et al. 2006; Neira et al. 2006; Cottet et al. 2007; Wang et al. 2010; Cutajar et al. 2012). As *Spartina* patches expand, algae are transformed into detritus and subsurface deposit feeders increase in abundance, while suspension feeders and detritivores decrease (Cutajar et al. 2012; Neira et al. 2006). Quantifying the impacts of plant invasion on benthic communities is important for understanding the underlying causes of invasion (Snelgrove 1998; Prieur-Richard et al. 2000; Wu et al. 2009). *Spartina* invasion was accompanied by decreased species diversity (H') and abundance of infauna inhabiting the seafloor (Neira et al. 2007; Tang and Kristensen 2010; Cutajar et al. 2012), and a substantial reduction in macrofauna species richness and diversity in northern Europe and Australia (Chen et al. 2007; Neira et al. 2007; Tang and Kristensen 2010), but had no impact on benthic invertebrates or fish in Tasmania, southeastern Australia (Hedge and Kriwoken 2000; Wu et al. 2009). Salt marsh restoration using *S. maritima* has been reported to increase the complexity (ecological diversity and species richness) and abundance of some benthic macroinvertebrate communities (Curado et al. 2014). However, few studies have examined the effect of *S. anglica* patch size and structure on benthic macrofauna.

In this study, we investigated the patch structure of early invasion *S. anglica* (<8 years of invasion history), and the impact on macrofauna communities in various habitat types. The objective of this study was to identify the structural characteristics of *S. anglica* in the early stage of invasion, to characterize its energy allocation pattern and determine the dispersal strategies of independent patches. Canonical correlation analysis (CCA) was conducted to evaluate the effects of *S. anglica* on macrobenthic distribution depending on its invasion habitat. We hypothesized that (1) *S. anglica* has the early invasion strategies to

allocated resource to root and rhizomes in order to settle in harsh environment and (2) its invasions negatively affect macrofaunal density, richness, and diversity. The results of this study offer significant insight into the early invasion strategies of the aggressive plant invader *Spartina*, which may facilitate coastal wetland management and sheds light on the impact of *Spartina* invasion on macrofaunal assemblages.

Materials and methods

Study area

This study was conducted in a tidal marsh in May 2016 in southern Dongmak-ri, Ganghwa Island, South Korea (37°35'36.97"N, 126°26'32.36"E) (Fig. 1). In 2017, the study area had a mean annual temperature of 11.74 °C (maximum, 6.88 °C;

minimum, 16.84 °C), total annual precipitation of 787 mm, mean wind velocity of 2.02 m/s, and total annual sunshine duration of 2274.2 h (Ganghwa weather station, Korea Meteorological Administration). Water speed was $\sim 67.96 \text{ m h}^{-1}$ and flooding durations were from ~ 1 (closest patch to Levee) to ~ 4 h (farthest patch to Levee) per tidal cycle (Shin et al. 2020) (Fig. 2). The longest distance between patches is 120 m and the slope of the shore was low (Fig. S1), such that flooding duration conditions are similar between the patches. Higher mud content was observed Ganghwa Southern Tidal Flat (Choi et al. 2010).

The three most common native marsh plant species at the study sites were *Suaeda japonica* Makino, *Triglochin maritimum* Linne, and *Phragmites communis* Trinius. *Suaeda japonica* vegetation was under colonization by *Spartina anglica* in both dense monotypic patches and meadows.

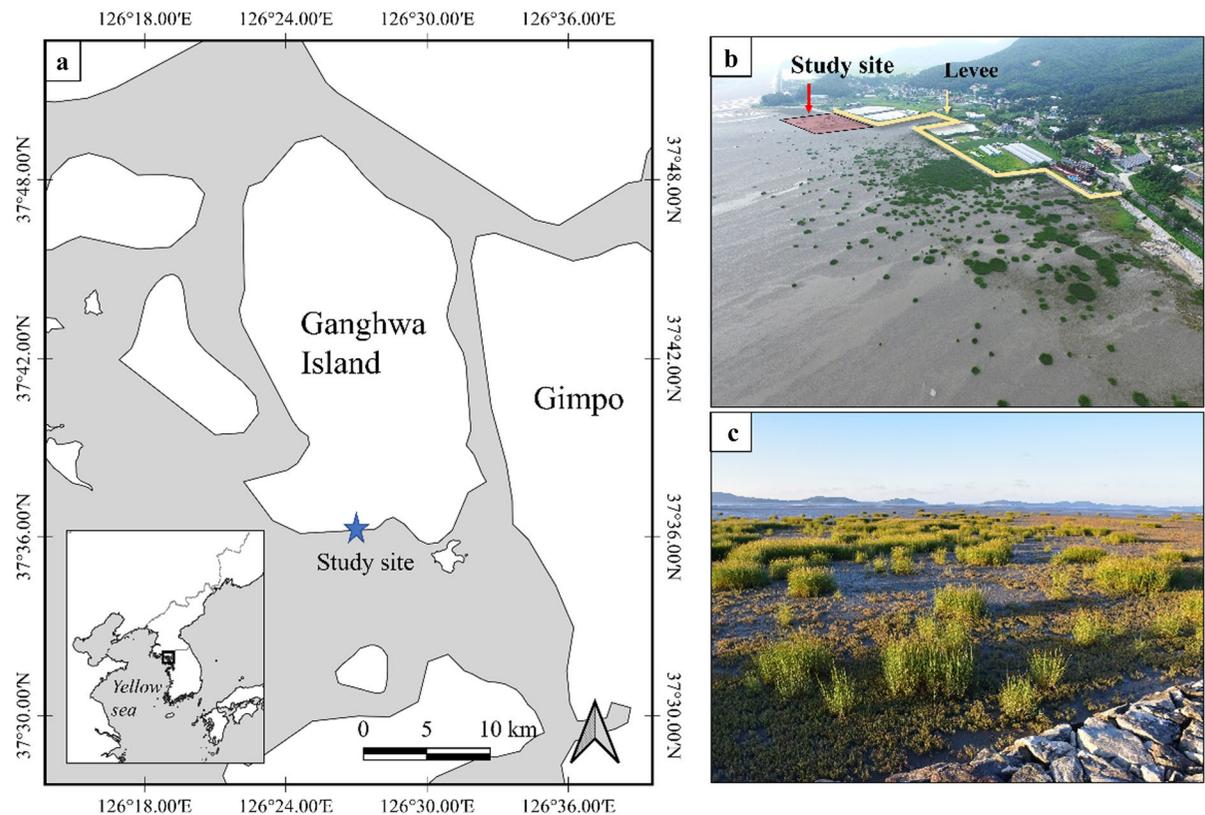


Fig. 1 **a** The study site at Dongmak-ri, Ganghwa Island, South Korea. **b** Aerial image of *Spartina anglica* meadow and patches captured by drone (height, 150 m; September 6, 2016). **c** *S. anglica* patches within *Suaeda japonica* vegetation (October 9, 2016)

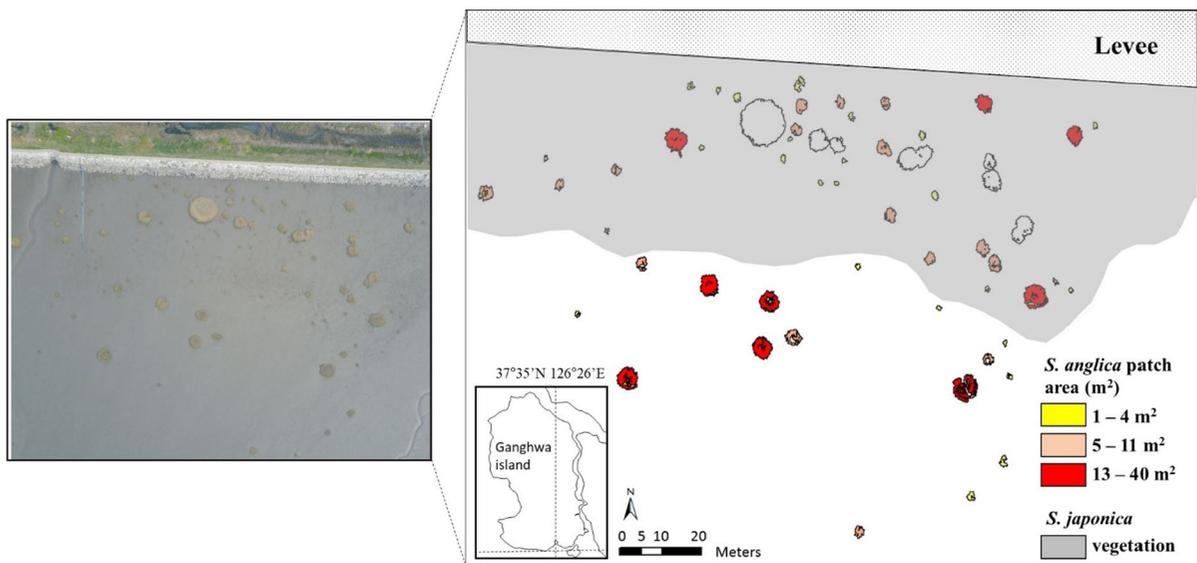


Fig. 2 *Spartina anglica* patches at the study area in Dongmak-ri, Ganghwa Island, South Korea. Colors indicate patch sizes on bare mudflats. Grey shading indicates *Suaeda japonica* vegetation

Vegetation survey

To investigate variation in *S. anglica* patch structure, we surveyed 24 *Spartina* patches near the levee (Fig. 2). To examine each patch independently, we included only those at distances of >2 m from all other patches to avoid obviously coalesced clumps (Casellanos et al. 1994). Neira et al. (2007) reported that changes in *Spartina* growth stages and macrofaunal communities were related to sediment and environmental properties. *Suaeda japonica* vegetation was observed at 0–60 m from the levee, and on bare mudflats without other vegetation at 60 m from the levee. Lateral expansion of *Spartina* tussock was highly correlated to its invasion period and its rate has consistency by *Spartina* hybrids (Gallego-Tévar et al. 2019). we assumed that every patch has lateral tussock growth and lateral expansion should not differ significantly due to environmental gradient such as elevation, hydrodynamics, sediment as study the patches of each class are randomly distributed in a narrow area of about 1 ha (Balke et al. 2012). Based on field observation, it has been identified that every patch had lateral tussock growth. Through stratified random sampling, we divided *S. anglica* patches into small (1–4 m²), medium (5–11 m²), and large (13–40

m²) size classes, with four replicates per habitat. We used a drone (Mavic Pro; DJI Co., China) to obtain photographs of the study site, which were converted into shapefiles using eCognition 64 software (Trimble, USA). Patch sizes were calculated using ArcGIS 10.1 software (Esri, USA).

In the field survey, we measured the circumference, and minimum and maximum diameter, of each *S. anglica* patch to validate the estimated patch sizes. Aboveground *S. anglica* shoots were harvested by clipping the vegetation at the sediment surface in quadrats (1 m \times 1 m). The density and the height of *S. anglica* were measured per quadrat. For the heights, we randomly sampled and recorded the heights of four shoots from each edge and one shoot from the center of each quadrat. Dead shoots and leaves were identified by their yellow or brown color (Darby and Turner 2008). All aboveground materials were stored in plastic bags in a refrigerator at 4 °C. Each individual was divided into stems and leaves, and then washed with water about 10 times to remove sediment. Living or dead plant material was placed in paper bags, dried at 80 °C for approximately 72 h, and then weighed to the nearest 0.01 g. Aboveground *Suaeda japonica* biomass was harvested and weighed following the same procedures. Belowground *S.*

anglica biomass (rhizomes and roots) was collected using a 10-cm-long polyvinyl chloride (PVC) core (diameter, 15 cm) (Figuroa et al. 2003). Two replicates of each soil core were collected in each quadrat. The samples were stored in plastic bags in a refrigerator at 4 °C. The segments were washed in a 500- μ m sieve to prevent loss of fine root materials. Belowground materials were separated into roots and rhizomes (Figuroa et al. 2003), which were placed in separate paper bags, dried at 80 °C for approximately 72 h, and weighed to the nearest 0.01 g.

Macrobenthic sampling

We collected 15-cm-diameter sediment cores to a depth of 10 cm for macrobenthic faunal analysis, with two replicates. In the laboratory, the cores were washed through 500- μ m mesh. Animals retained on the sieve were preserved in 70% ethanol, sorted, counted and weighed to the nearest 0.001 g, and identified to the lowest possible taxonomic level using a dissecting or compound microscope. As a control group, we randomly selected and sampled bare mudflats and patches of *Suaeda* vegetation 1 m from the *Spartina* patches; sampling followed the procedures described for *S. anglica*.

Bottom sediment analysis

To analyze sediment characteristics, we collected sediment samples at a depth of 5 cm and isolated 300 g of sediment from those of macrobenthic sampling. We dried 5 g of each isolated sediment at 105 °C for 24 h to determine its water and ash content, and at 550 °C for 4 h to determine its organic content. We mixed 7 g of air-dried soil with 35 mL distilled water to obtain a suspension, which was subjected to shaking at 180 rpm for 30 min and centrifugation at 3000 rpm for 1 min. We measured salinity and pH using a PC-2700 system (Thermo Eutech, Singapore) fitted with the CONSEN9201J and ECFG7370101B probes, respectively. $\text{NH}_4\text{-N}$ in sediment was extracted with a 2 M KCl solution, and $\text{PO}_4\text{-P}$ was extracted with Bray No. 1 solution (Bray and Kurtz 1945). $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ in the extracted soil solutions were analyzed using the indophenol (Murphy and Riley 1962) and ascorbic acid reduction (Solorzano 1969) methods, respectively.

Statistical analyses

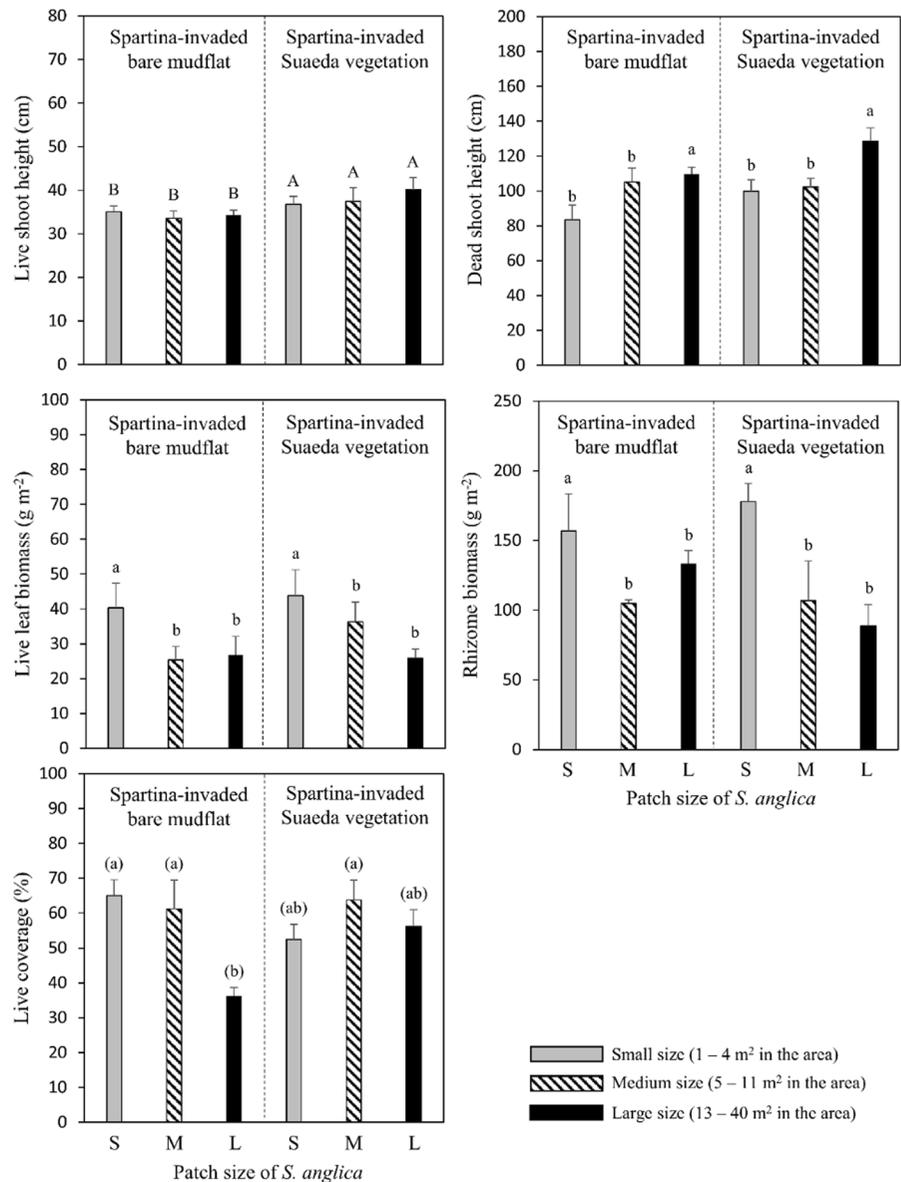
Several assemblage indices were calculated to compare benthic macrofaunal assemblages, including species richness, density, Shannon–Wiener H' , and biomass (Pielou 1966). The normality tested with Shapiro–Wilk test and its homogeneity by Levene's test to ensure parametric statistic validity. Differences in macrobenthic faunal assemblage indices, environmental variables among habitats (bare mudflats, *Spartina*-invaded bare mudflats, *Suaeda* vegetation, and *Spartina*-invaded *Suaeda* vegetation) were tested by one-way analysis of variance (one-way ANOVA). In addition, differences and the interaction in *S. anglica* patch structures among the habitats and patch sizes (small, medium, and large) were tested by two-way ANOVA. Tukey's honestly significant difference (HSD) was used for multiple comparison procedure. Non-parametric Kruskal–Wallis test was used when normal distribution of the residuals was not assumed. Canonical correspondence analysis (CCA) was performed to examine the relationships between macrofaunal assemblage and environmental variables. All analyses were conducted using R v3.3.2 software (R Development Core Team, Austria).

Results

Spartina anglica density, height, coverage, and biomass

Characteristics of *S. anglica* according to patch size and habitat were investigated to understand its growth strategy. Living and dead shoot density ranged from 173.5–227 to 163.25–225.75 shoot m^{-2} , respectively. Living and dead shoot height ranged from 33.55–40.10 to 83.45–128.7 cm, respectively. Living organ coverage ranged from 36.25–65% m^{-2} (Table S1). No discernable patterns were observed among patch sizes and habitats in terms of average living or dead shoot density ($P > 0.05$) (Table S2). Living *S. anglica* shoot height was significantly higher among *Suaeda japonica* vegetation than in the adjacent bare mudflats ($P < 0.05$) (Fig. 3). Dead shoot height was significantly higher among large than small *S. anglica* patches ($P < 0.05$) (Fig. 3). Living *S. anglica* coverage showed an interaction effect

Fig. 3 Relationships between living and dead *Spartina anglica* biomass and patch size for *Suaeda japonica* vegetation, and for bare mudflats in Donggeom-ri, Ganghwa Island, South Korea. Error bars indicate standard error of the mean. Different letters indicate significant differences between habitats (capital letters) or among *S. anglica* patch sizes (small letters) according to two-way analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) test or the Kruskal–Wallis test ($P < 0.05$, $n = 4$). Brackets indicate an interaction between patch size and habitat



according to the invaded habitat ($P < 0.05$) and patch size ($P < 0.001$). The large-sized patch had the lowest coverage value in *Spartina*-invaded bare mudflat (Fig. 3). Living aboveground and belowground *S. anglica* biomass ranged from 42.91–57.21 to 176.89–302.22 g m^{-2} , respectively. Aboveground biomass corresponded to 16–23% of the belowground biomass. Living leaf biomass and rhizome biomass differed significantly by patch size and habitat type (Fig. 3). Rhizome biomass was significantly higher in small than medium and large *S. anglica* patches

($P < 0.001$). Dead leaf biomass was significantly higher among *Suaeda japonica* vegetation than on the bare mudflats. The ratio of below- to above-ground biomass was significantly higher in small *S. anglica* patches (Fig. 4).

Macrobenthic community survey

In the present study, significant changes in the macrofauna community by the patch size were not found. However, we found that benthic macrofaunal

Fig. 4 Variation in above- and below-ground biomass, by *S. anglica* patch size. Error bars indicate standard error of the mean. Different letters indicate significant differences according to one-way ANOVA and Tukey's HSD test ($P < 0.05$, $n = 8$)

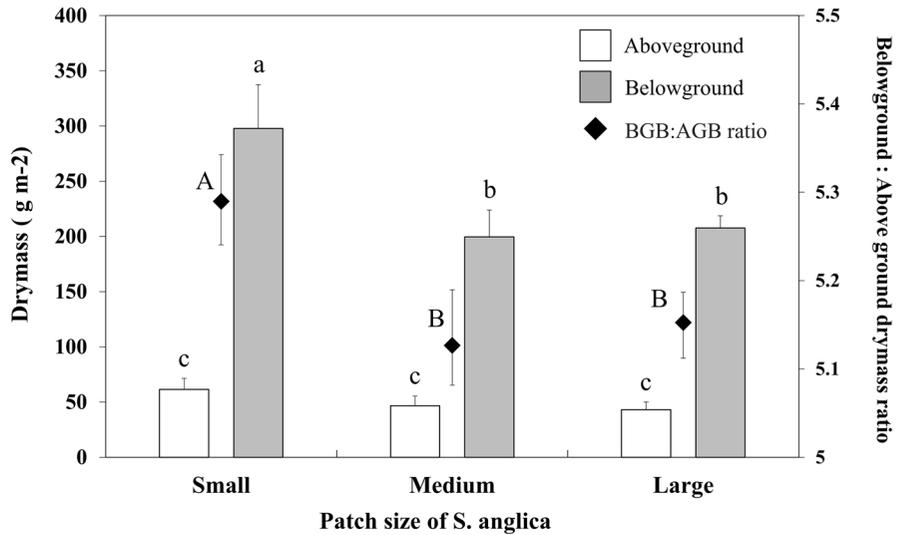


Table 1 Species density and richness (/m²) in bare mudflat and *Suaeda* vegetation habitats (all samples combined)

	Bare mudflats		<i>Suaeda</i> vegetation	
	No invasion	<i>Spartina</i> invasion	No invasion	<i>Spartina</i> invasion
Annelida				
<i>Eteone</i> sp. (I)	2.83	0	0	0
<i>Glycera macintoshi</i> (I)	0	0	2.83	0
<i>Glycinde gurjanovae</i> (I)	0	0	5.66	0
<i>Mediomastus californiensis</i> (I)	152.79	0	107.52	8.49
<i>Nephtys chemulpoensis</i> (I)	8.49	2.83	19.81	0
<i>Oligochaeta</i> sp. (I)	11.32	0	2.83	0
<i>Paraleonnates uschakovi</i> (I)	0	0	2.83	0
<i>Perinereis lineata</i> (I)	84.88	31.12	42.44	135.81
Total density	260.31	33.95	183.91	144.3
Species richness	5	2	7	2
Mollusca				
<i>Batillaria cumingi</i> (E)	0	0	0	2.83
<i>Estellacar galactodes</i> (I)	2.83	0	2.83	0
<i>Glaucanome chinensis</i> (I)	2.83	0	0	2.83
<i>Lactiforis takii</i> (E)	0	8.49	2.83	0
<i>Laternula marilina</i> (I)	67.91	0	45.27	5.66
<i>Moerella rutila</i> (I)	2.83	0	0	0
<i>Potamocorbula</i> sp.(I)	0	5.66	0	0
Total density	76.39	14.15	50.93	11.32
Species richness	4	2	3	3

E Epifauna; I infauna

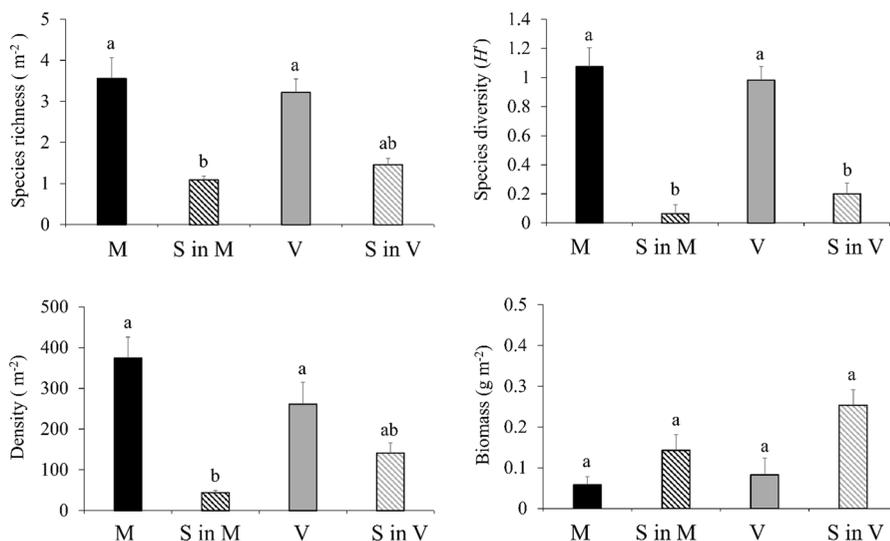
assemblages was strongly affected by *Spartina* invasion. A total of 16 benthic macrofauna was identified from four habitats: bare mudflats, *Spartina*-invaded bare mudflat, *Suaeda* vegetation, and *Spartina*-invaded *Suaeda* vegetation. The highest macrobenthic species richness appeared in *Suaeda* vegetation (10 species; Table 1). However, bare mudflats had the highest total macroinvertebrate density, with 119 individuals m^{-2} , consisting predominantly of the capitellid deposit feeder *Mediomastus californiensis*. Bare mudflats and *Spartina*-invaded *Suaeda* vegetation yielded fewer species (four and five, respectively), and were dominated by the nereidid deposit feeder *Perinereis linea*. Lower Annelida and Mollusca species richness and density were observed in *Spartina*-invaded habitats. Among polychaete annelid populations, *Mediomastus californiensis* showed the greatest reduction under *Spartina* invasion. Among molluscan populations, the laternulid bivalve *Laternula gracilis* showed the greatest decrease. Nine species found in habitats with no *Spartina* invasion were absent from *Spartina*-invaded habitats, whereas the epifaunal gastropods *Batillaria cumingi* and *Lactiforis takii* were found in *Spartina* patches.

Macrobenthic species richness was 70% lower in *Spartina*-invaded bare mudflats than in bare mudflats without *Spartina* invasion; *Spartina* patches reduced the species richness of polychaete annelids to a greater extent than that of mollusks (Fig. 5). The mean H' was >80% lower in *Spartina* patches

than bare mudflats without invasion. The mean H' was 94% lower in *Spartina* patches than *Suaeda* vegetation without *Spartina* invasion. *Spartina* patches reduced the diversity of annelids to a greater extent than mollusks (Table 1). Overall, mean species richness and density were significantly lower in *Spartina* patches, whereas no significant difference was detected between bare mudflats and *Suaeda* vegetation without *Spartina* invasion (Fig. 5).

CCA ordination results were based on macrobenthic density data and six environmental variables: organic matter, NH_4 -N, and PO_4 -P content, pH, salinity, and belowground biomass (Fig. 6). The variance explained by the first two CCA axes was 51.34% and 26.81%, respectively (78.15% in total; Table 2). The first axis was significantly related to pH (factor loading=0.6387) and belowground biomass (factor loading=-0.9453) (Table 2), whereas the second axis was significantly related to NH_4 -N content (Table 2). From right to left on the first CCA axis, the macrofaunal assemblages showed zonation from bare mudflats and *Suaeda japonica* vegetation to *S. anglica*-invaded mudflats and *S. anglica*-invaded *Suaeda japonica* vegetation (Fig. 6). In both mudflats and *Suaeda japonica* vegetation areas, zones with and without *S. anglica* invasion were clearly distinguished (Fig. 6), with *S. anglica* invasion zones showing higher organic matter content, salinity, and belowground biomass, and lower pH, than zones without invasion.

Fig. 5 Mean species richness, species diversity (H'), species density, and biomass of total macrofauna for samples in four habitats: bare mudflats (M), *Spartina*-invaded bare mudflats (S in M), *Suaeda* vegetation (V), and *Spartina*-invaded *Suaeda* vegetation (S in V). Error bars indicate SEM ($n=9$ for M, V; $n=12$ for S in M, S in V). Different letters indicate significant differences among habitats according to one-way ANOVA and Tukey's HSD test ($P<0.05$)



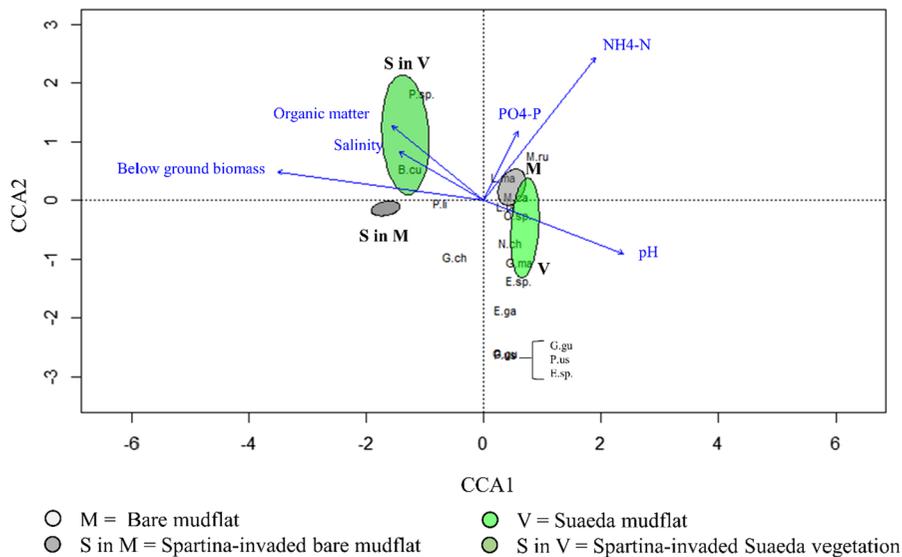


Fig. 6 Canonical correspondence analysis (CCA) ordination of four macrofaunal assemblages and six environmental variables from the sampling site at Dongmak-ri, Ganghwa Island (n=9 for M, V; n=12 for M with S, and V with S). Zonation was determined according to the standard error (SE). E.sp, *Eteone* sp.; G.ma, *Glycera macintoshi* G.gu, *Glycinde gurjanovae*;

M.ca, *Mediomastus californiensis*; N.ch, *Nephtys chemulpoensis*; O.sp., *oligochaeta* sp.; P.us, *Paraleonnates uschakovi*; P.li, *Perinereis lineae*; B.cu, *Batillaria cumingi*; E.ga, *Estellacar galactodes*; G.ch, *Glauconome chinensis*; L.ta, *Lactiforis takii*; L.ma, *Laternula marilina*; M.ru, *Moerella rutile*; P.sp., *Potamocorbula* sp.

Table 2 Factor loadings of variables obtained by canonical correspondence analysis (CCA)

	CCA1	CCA2
Organic matter	-0.4199	0.3435
NH ₄ -N	0.5127	0.6557
PO ₄ -P	0.1575	0.3174
pH	0.6387	-0.2434
Salinity	-0.3880	0.2218
Belowground biomass	-0.9453	0.1326
Proportion of variance	0.5134	0.2681
Cumulative proportion	0.5134	0.7815
Eigenvalues	0.3819	0.1994

Zonation was determined at standard error (SE) > 0.600 (bold)

Discussion

Spartina anglica density, height, coverage, and biomass

Our results showed that the structural characteristics of invading *Spartina* patches, including living leaf biomass, rhizome biomass, and coverage, were

dependent on *Spartina* patch size. Small patches had significantly higher rhizome biomass than medium-sized and large patches at depths of 0–10 cm. Patch size is related to invasion history; smaller patches indicate a shorter invasion history (Gallego-Tévar et al. 2019). In addition, we found there was no significant relationship between the *Spartina* patch size and the sampled habitat characteristics (Fig. S2). Therefore, we assume that changes to *S. anglica* structural characteristics occur after invasion and spread throughout the patches.

At the study area, *S. anglica* patches with a short invasion history allocated resources to roots and rhizomes, to settle early populations and adapt to harsh environmental stresses such as high salinity and tides. Schubauer and Hopkinson (1984) also reported that rhizomes accounted for a greater portion of belowground biomass in a Georgia salt marsh. Investment of resources into rhizomes is crucial for the invasion of clonal plants, such as *S. anglica*, allowing them to adapt to a wide range of habitats by maintaining soil volume (Petrone et al. 2001). If belowground organic matter accumulation is insufficient, marshes with abundant aboveground plants can rapidly become

open water, as accumulated sulfide causes plant death. Clonal integration is an important means of population expansion for the invasive *Phragmites australis*, which would otherwise be confined to higher-elevation marshes due to low oxygen availability at lower elevations (Amsberry et al. 2000).

Aboveground and belowground biomass allocation are important for marsh ecosystem structure and function, because they influence various processes such as carbon sequestration, gas transport, nutrient cycling, and ecosystem resilience (Darby and Turner 2008; Tripathee and Schafer 2014; Castillo et al. 2016). The ratio of below- to above-ground biomass was significantly higher in small *Spartina* patches, suggesting differential carbohydrate use under harsh environmental condition (Castillo et al. 2016) despite its small range (0.13–0.16). In spring, high root and rhizome biomass can affect leaf biomass. *Phragmites australis*, *Egertian densa*, and *Myriophyllum* show depleted carbohydrate reserves in the rhizomes during rapid growth (Costa et al. 2003). *Spartina alterniflora* showed evidence of biomass translocation from below- to above-ground early in the growing season, when aboveground growth is at its maximum (Connor and Chmura 2000). However, the ratio of below- to above-ground biomass differed significantly according to settlement history and location within the marsh (Valiela et al. 1976; Roman and Daiber 1984). Dame and Kenney (1986) reported an average net aboveground primary production of 2188 and 1295 g m⁻² year⁻¹ at low and high elevations within the marsh, respectively, whereas the corresponding average net belowground primary production rates were 2363 and 5445 g m⁻² year⁻¹. In the present study, ratio of below- to above-ground biomass significantly is significantly high in small size patch of *Spartina* in mud flat and high elevation having a wave exposure time of less than 4 h. In a similar environment, the structural characteristics of *Spartina* invasions might be observed. However, since South Korea has only one research site related to patch size of *Spartina*, it is necessary to validate ratio of below- to above-ground biomass according to the size of the patch at other sites. Ellison et al. (1986) also reported decreasing root and rhizome penetration (<20 cm) into the marsh substrate with increasing tidal height, and belowground biomass reached a maximum at the marsh edge. In the present study, rhizomes sampled at depths of 6–9 cm were often curved, returning to the

surface layer where they could become shoots. This finding indicates that depth should be considered as a major factor for the eradication of *Spartina*. *Spartina densiflora* is a halophyte with high salinity tolerance, but its growth is limited in halosaline conditions (Castillo et al. 2016). In the present study, salinity was not directly related to *S. anglica* biomass accumulation in any habitat; therefore, *S. anglica* may have greater salinity tolerance than *S. densiflora*.

Spartina invasion showed distinctive invasion strategies to spread out in short distance. The very first invasion of *Spartina* could be seed-mediated in long distance, but once, *Spartina* started to establish in proper environment, they invested more energies and resources into their belowground parts such as rhizomes. Then, *Spartina* were able to spread out in more harsh condition by increasing their patch sizes. Due to this plasticity and adaptive strategies, *Spartina* seems to become successful invaders worldwide. It indicates broad insight that invasive plants such as *Spartina* and *Phragmites australis* are jack of all trades rather than master of some (Richards et al. 2006). Our findings could be translated to valuable management guidelines for coastal managers to be aware of and deal with the harmful impacts of *Spartina* invasion. Since early invasion of *Spartina* was associated with increased belowground biomass, it would be necessary to conduct soil tillage to destroy rhizome to control *Spartina* invasions.

Effect of *Spartina* invasion on macrobenthic communities

Intertidal macrobenthic communities usually vary by habitat type and tidal level (Hosack et al. 2006; Bouma et al. 2009; Compton et al. 2013). In the present study, the effects of *Spartina* on macrobenthic communities was estimated and compared to those in adjacent habitats. Plant introductions to salt marsh systems result in significant changes, ranging from species replacement to widescale alteration of ecosystem properties; these altered physical and chemical environments can also strongly influence the recruitment, survival, growth, and reproduction of benthic invertebrates in invaded areas. (Neira et al. 2005; Grosholz et al. 2009). Neira et al. (2005) observed 75% lower total macrofaunal density, and lower species richness, in *Spartina*-vegetated sediments representing 30-year-old invasion at

Elsie Roemer Bird Sanctuary (California, USA) than in an adjacent unvegetated tidal flat. Differences in macrofaunal community structure have been shown to be greater among tidal elevations than between native halophyte and invasive *Spartina* communities in Chinese estuarine *Spartina*-invaded tidal flats (Chen et al. 2009). The present study also revealed a significant association between *Spartina* invasion and macrofaunal assemblages. We observed macrofaunal changes in bare mudflats and *Suaeda* vegetation invaded by *Spartina*, including low species richness, H', and macrofaunal density; more epifauna in *Spartina*-invaded bare mudflats; higher density of the subsurface deposit-feeding nereidid polychaete *Perinereis linea* in *Spartina*-invaded *Suaeda* vegetation; and no significant difference in macrobenthic biomass among habitats. *Spartina* invasion also affected macrobenthic communities depending on the invasion history, which was estimated to be 2–8 years at the study site. Even within such a short period, the impact of *S. anglica* on macrofaunal diversity and density was sufficiently strong to produce significant effects despite no significant *Spartina* invasion effect by patch size (less than 40 m²) on macrofauna community. To some extent, these results are consistent with previous findings obtained in a temperate Australian salt marsh (Cutajar et al. 2012), and in Wenzhou Bay, China (Ge et al. 2012). Cutajar et al. (2012) reported that invaded patches showed a 50% reduction in species richness, and reduced diversity, compared to two uninvaded habitats. Ge et al. (2012) demonstrated that macrobenthic communities were more complex in initial *S. alterniflora* invasion patches than in patches at other invasion stages, and that *S. alterniflora* invasion stage significantly affected macrobenthic community structure; their results also indicated higher biodiversity in the initial stage of invasion (1–2 years), decreasing during invasion progress (3–4 years) until completion (5–6 years), perhaps due to *S. alterniflora* canopy changes. Macrofaunal density in the *S. anglica* patches of the present study was also lower than that in native marsh (by 60%), but not significantly different from that in the bare mudflats. We observed no differences in biomass among habitats. However, the results might be a product of either co-occurrence with *Suaeda* vegetation or tidal height.

Our CCA results indicated that the key environmental factors driving macrobenthic community changes were belowground biomass, organic matter

content, salinity, and pH (Fig. 6). *S. anglica* invasion was associated with low pH, high organic matter content, high belowground biomass, and high salinity. These results are consistent with those of previous studies reporting changes in the physicochemical properties of sediment habitats under *Spartina* invasion (Neira et al. 2007). The macrofaunal diversity and density of tidal flat environments increase significantly when ecosystem engineers, such as oyster reef or seagrasses, are present because they create and modify habitat structures (Brusati and Grosholz 2006). In this study, comparison of macrofauna assemblages between habitats with and without *Spartina* patches showed clear trends (Fig. 6). Macrofaunal H' was higher in bare mudflats and native marsh than in habitats containing *Spartina* patches. *Spartina* patches yielded low macrofaunal diversity, low and richness in mudflats (Hedge and Kriwoken 2000). However, the infaunal polychaete *P. linea*, and the epifaunal gastropods *B. cumingi* and *L. takii*, were enhanced in *Spartina* patches. These findings are similar to previous reports of increased macrofaunal dominance with a shift in feeding mode from surface microalgal feeding to subsurface detritus feeding (Neira et al. 2007; Bouma et al. 2010), which creates *Spartina*-free areas in open mudflats (Brusati and Grosholz 2009). In a study examining the influence of *Spartina* marshes and detritus availability on the spatial structure and temporal variability of macrobenthic associations, Netto and Lana (1999) suggested that spatial and temporal shifts among infaunal organisms may be more evident than those of mobile epibenthic forms.

Our study area contained no 2-cm-diameter burrows among *Spartina* patches, which indicates the absence of large decapod crustaceans; we also observed a higher density of Annelida than Mollusca organisms. *Spartina* patches appeared to facilitate the colonization of oligochaetes at higher elevations, while also inhibiting taxa such as crustaceans and bivalves. However, macrofauna biomass did not differ significantly between habitats with and without *Spartina*. This result is consistent with the findings of a study on the effects of *Spartina* invasion on benthic macrofaunal assemblages in an Australian salt marsh (Cutajar et al. 2012), but not with those of previous studies that found a negative correlation between root biomass and macrofaunal biomass (Forbes and Lopez 1990; Wang et al. 2010).

Our CCA results clearly showed that *Spartina* invasion was a key factor in macrofaunal distribution (Fig. 6). When belowground biomass was sufficient, macrofauna diversity, density, and richness decreased to a greater extent among *Spartina* patches, whereas a few species, such as epifauna, remained dominant. Macrofauna species may have been depleted compared to both native marsh and bare mudflats due to the belowground biomass of roots and rhizomes. Our CCA results also indicated that organic matter content, salinity, and pH can be considered as crucial factors for community organization. Benthic deposit feeders assimilate resuspended benthic diatoms from bulk particulate organic matter (Kang et al. 2003; Kanaya et al. 2008). Despite the high salinity tolerance of *S. densiflora*, its growth is limited under halo-saline conditions; we found that salinity was positively related to belowground *S. anglica* biomass. Lee et al. (2016) demonstrated the high invasion potential of hybrid *Spartina* genotypes due to their strong salinity tolerance; plants under high salinity conditions had a significantly greater root to shoot biomass ratio than those under either low or medium salinity conditions. Interactions between pH and salinity are important for evaluating *Spartina* responses in nutrient culture and salt marsh experiments (Linthurst and Blum 1981).

In conclusion, we investigated the effects of *S. anglica* patch size in a range of tidal flat marsh habitats, to understand its reproductive strategies throughout the invasion process and its influence on macrobenthic communities. Smaller *Spartina* patches, which indicate a shorter invasion history (1–2 years), allocated more resources to rhizomes than larger patches, to adapt to the harsh tidal environment. *Spartina* invasion reduced macrofaunal species richness, diversity, and density, but may have enhanced epifauna in the tidal flat marsh. Macrofaunal assemblages may have been negatively impacted in habitats under *Spartina* invasion; however, the results differed among habitat types. This study focused on early invasion *Spartina* patches rather than established meadows, to understand its initial asexual reproductive strategies and effects on macrofauna. Our results indicate that rhizomes in early *S. anglica* patches represent an important means of population expansion from favorable to unfavorable environments. Early

detection and a rapid response are key for managing *Spartina* invasion, particularly within 5 years, when *S. anglica* invasion has a major negative impact on native macrobenthic communities. Our findings could be translated to valuable management guidelines for coastal managers to be aware of and deal with the harmful impacts of *Spartina* invasion. Since early invasion of *Spartina* was associated with increased belowground biomass, it would be necessary to conduct soil tillage to destroy rhizome to control *Spartina* invasions. Further studies should perform long-term (> 10 years) monitoring of *Spartina* invasion patterns and structural characteristics, and assess the impact on surrounding macrobenthic communities.

Acknowledgments The authors would like to thank the member of Laboratory of Plant Ecology, including Jeong Hwan Bang, Saeromi Moon, Seung-Kyung Lee, Hyunyoung Yang, Shinyeong Park, Minjin Choi, Youngeun Kim for assistance with the vegetation survey. We also thank Tai Yang Lim and Yong Hwan Kim for their assistance in data acquisition using UAV. We would like to express a great appreciation to the anonymous reviewers for their valuable comments on previous versions of this manuscript.

Funding This work was supported by the Korea Environment Industry and Technology Institute (KEITI) through the Urban Ecological Health Promotion Technology Development Project, funded by the Korea Ministry of Environment (MOE) (no. 2020002770002). This work is financially supported by Korea Ministry of Land, Infrastructure and Transport (MOLIT) as Innovative Talent Education Program for Smart City. This work was supported by the National Research Foundation of Korea (NRF) Grant funded by the Korea government. (MSIT) (2022R1A2C1003504). Wonhyeop Shin is grateful for financial support from Hyundai Motor Chung Mong-Koo Foundation.

Data availability All data produced in this study are available upon requests from the corresponding author.

Code availability ‘Not applicable’ for that section.

Declarations

Conflict of interest The authors declare no conflict of interests nor competing interests.

Ethical approval Sampling protocols were established in compliance with the ethical standards.

Consent to participate All persons entitled to authorship have been so named and have agreed to participate.

Consent for publication All authors have seen and agreed to the submitted version of the manuscript.

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