

# Grazer host density mediates the ability of parasites to protect foundational plants from overgrazing

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## Abstract

Like many top consumers, parasites can regulate feeding of their prey via trait-mediated means. If parasites modify the feeding behavior of ecologically important grazers, they may have cascading effects on the structure and functioning of whole plant communities. The extent to which parasites can influence plant communities in this way is largely dependent on the strength of their behavioral alteration, their prevalence in host grazers, and the density of those hosts. Recent experiments and comparative surveys in southeastern USA salt marshes revealed that common larval trematode parasites suppress the per capita grazing impacts of the marsh periwinkle (*Littoraria irrorata*), generating a trophic cascade that protects foundational marsh plants from drought-associated overgrazing. Here, we conducted a field manipulation wherein we modified grazer host density while holding infection prevalence constant at an ecologically relevant level (20%) to determine whether the indirect, facilitative effects of parasites on marsh plants varied with the density of grazers. We found that parasites had significant positive impacts on marsh net primary productivity at moderate densities of snails ([?]50 snails/ 0.5 m<sup>2</sup>), but that the positive effects of parasites were negligible at lower densities. Our results confirm the findings of previous studies that parasites can protect marsh plants from overgrazing at sufficiently high prevalence, but show that their ability to do so depends on host density.

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Like many top consumers, parasites can regulate feeding of their prey via trait-mediated means. If parasites modify the feeding behavior of ecologically important grazers, they may have cascading effects on the structure and functioning of whole plant communities. The extent to which parasites can influence plant communities in this way is largely dependent on the strength of their behavioral alteration, their prevalence in host grazers, and the density of those hosts. Recent experiments and comparative surveys in southeastern USA salt marshes revealed that common larval trematode parasites suppress the per capita grazing impacts of the marsh periwinkle (*Littoraria irrorata*), generating a trophic cascade that protects foundational marsh plants from drought-associated overgrazing. Here, we conducted a field manipulation wherein we modified grazer host density while holding infection prevalence constant at an ecologically relevant level (20%) to determine whether the indirect, facilitative effects of parasites on marsh plants varied with the density of grazers. We found that parasites had significant positive impacts on marsh net primary productivity at moderate densities of snails ([?]50 snails/ 0.5 m<sup>2</sup>), but that the positive effects of parasites were negligible at lower densities. Our results confirm the findings of previous studies that parasites can protect marsh plants from overgrazing at sufficiently high prevalence, but show that their ability to do so depends on host density.

## Introduction

A sizable body of research has been devoted to the role of top predators in organizing communities and increasing ecosystem stability through trait-mediated or density-mediated control of herbivorous prey populations (Beschta & Ripple 2009, Estes et al. 2011, Rosenblatt et al. 2013, Ripple et al. 2014). Though small, parasites can also regulate grazer populations and trigger trophic cascades, with powerful ramifications for the structure and functioning of natural communities (Wood et al. 2007, Buck & Ripple 2017, Morton & Silliman 2020). In fact, because parasites can initiate trait-mediated indirect effects via both consumptive and nonconsumptive pathways, they may be even more likely than predators to trigger trait-mediated trophic cascades (Buck & Ripple 2017, Buck 2019). Unlike predators, however, parasites only attack one host per life stage, meaning that the potential for parasites to exert trait-mediated influence on ecosystems is largely a function of the number of infected hosts (Buck 2019). The extent to which parasites alter the structure and functioning of ecological communities through cascading trait-mediated indirect effects necessarily depends on the myriad processes that underlie disease transmission, the specifics of the host traits being modified, and the ecological context in which those traits are expressed. While there are many well-publicized examples of parasites inducing dramatic changes in the behavior or appearance of their host species, most changes to host traits take the form of subtle alterations to behaviors such as feeding and locomotion. Any detectable cascading effects as a result of these subtle changes may only emerge when conditions favor high infection prevalence/intensity. However, if the ecological influence of host behavior scales with host density, the effects of parasites at a given prevalence may not be detectable at high host densities when the aggregate ecological impacts of hosts drown out the aggregate effects of parasites. Likewise, it may be difficult to discern the influence of parasites at low host densities when the ecological impacts of host behavior are negligible.

In southeastern USA salt marshes, the keystone gastropod *Littoraria irrorata* (hereafter referred to as snails or grazers) can form high-density consumer fronts ( $\sim 100\text{--}1000$  snails/m<sup>2</sup>) in response to sublethal drought stress that weakens plant defenses (Silliman et al. 2005). High densities of grazing snails can yield cascading vegetation loss even after the initiating drought stress has passed, converting large swaths of highly productive marsh into relatively unproductive mudflat habitats (Silliman et al. 2005, 2013). In this system, parasitism by larval digenean trematodes can be prevalent among snails within these consumer fronts ( $>30\%$ ), likely because the mudflat areas generated by overgrazing are attractive to birds, which are definitive hosts of these trematodes (Morton 2018, Morton & Silliman 2020, Sharp & Angelini 2020). Previous experiments and observational studies revealed that one common trematode, *Parorchis acanthus*, can increase plant ecosystem resistance to die-off from drought-associated overgrazing by reducing per capita grazing rates of snails (Morton 2018, Morton & Silliman 2020).

Both infection prevalence ( $0 - >40\%$ ) and density ( $\sim 50\text{--}2000$  snails/m<sup>2</sup>) of adult snails vary considerably within marsh die-off areas throughout the southeastern USA (Silliman & Zieman 2001, Angelini et al. 2015, Morton & Silliman 2020). Thus, the ability of trematode parasites to confer ecosystem resistance to snail overgrazing is likely highly context dependent. Previous field manipulations of *P. acanthus* prevalence found that infection prevalence was roughly proportionate to reductions in the top-down impacts of grazers on marsh plants (Morton & Silliman 2020). Consistent with this, multi-site surveys found that the magnitude of grazer-induced damage (radular wounds) to plants along die-off borders decreased with increased prevalence of infection. Damage also increased with snail density (Morton & Silliman 2020). These results suggest that the ability of parasites to ameliorate stress and slow the rate of die-off expansion is likely dependent on both infection prevalence and grazer density, but the latter has yet to be experimentally tested. Therefore, a more robust understanding of how this parasite operates as an agent of ecosystem resistance in this system necessitates determining at what levels of host density parasites are likely to generate cascading trait-mediated impacts.

Here, we experimentally determine at which host densities parasites effectively ameliorate snail impacts on marsh vegetation via trait-mediated indirect effects. We did so by manipulating the density of grazer hosts in the field while holding infection prevalence constant at an intermediate value. We predicted that at high grazer densities, any ameliorating effects of parasitism on marsh plants would be overwhelmed by the magnitude of snail grazing. At low grazer densities, we predicted that parasitism would not lead to meaningful reductions in snail grazing that would translate to positive effects on plant growth and reproduction.

We anticipated that parasites would be most effective at increasing ecosystem resistance to overgrazing at moderate snail densities, where grazers' top-down impacts on marsh vegetation are just beginning to emerge.

### Methods

To determine how trematode infection influences marsh productivity at different levels of grazer host density, we conducted a field manipulation where we modified grazer host density while keeping infection prevalence constant. In June 2016 we established 0.5 m<sup>2</sup> caged plots in a structurally homogenous swath of smooth cordgrass (*Spartina alterniflora*) marsh within the Hoop Pole Creek Clean Water Reserve in Atlantic Beach, North Carolina, USA (34°42'25.12" N, 76°45'1.14" W). The site was characterized by a relatively uniform elevation, very low snail densities (<1 adult snail per m<sup>2</sup>) and minimal visible signs of snail grazing.

Snails used in the experiment were collected from a marsh die-off area where snails were abundant and infection prevalence was known to be high (Morton & Silliman 2020). Collected adult snails (shell length > 15mm) were transported back to the lab where their infection status was determined using a previously described cercariae shedding method that produces no false-positives (Morton 2018, Morton & Silliman 2020). We marked the shell of each infected snail with a red dot using a non-toxic, water resistant paint pen while uninfected snails were marked with a blue dot (Henry & Jarne 2007). Snails were kept in separate aquaria and provisioned with damp cordgrass wrack for ~3 weeks until they were deployed in the field.

Roofless cages (0.7 × 0.7 × 1 m) were constructed from untreated wooden posts and galvanized hardware mesh. A strip of copper tape was applied to the inner base of each cage, just above the sediment, to discourage snail escapes. Caged plots were spaced at least 1-m apart to assure independence of replicates—a design confirmed from past studies (Silliman & Zieman 2001, Silliman & Bertness 2002, Morton & Silliman 2020). Cages were buried 10-cm into the substrate to prevent snail and mud crab migration in and out of cages, and to inhibit belowground connections between plants inside and outside of the cages. Each plot was assigned to one of 8 snail density treatments (20, 40, 50, 60, 70, 80, 90, and 100 snails/per 0.5 m<sup>2</sup>) and one of two parasite addition treatments (0 and 20% infection prevalence). This resulted in 16 total treatments (n = 4 replicates per treatment). The snail densities used spanned the full range of adult snail densities observed within marsh die-off areas at this site. The 20% infection prevalence used in the experiment reflected the average naturally occurring summertime infection prevalence value for snails within local die-off areas (Morton & Silliman 2020). Uncaged plots marked at the corners with colored PVC flags (n = 4) and partial cages with one open side (n = 4) served as cage controls.

Before the beginning of the experiment, we removed any mud crabs and snails from cages. We took measurements of several marsh characteristics in all plots at the beginning of the experiment. We counted all *S. alterniflora* stems and measured the heights of ten randomly selected stems in each plot. Random selection of stems was accomplished by tossing a plastic dowel into plots and measuring the first 10 stems touching the dowel. We constructed a height-to-biomass regression by collecting 30 cordgrass stems of varying sizes from the marsh directly adjacent to our experimental site. The stems were washed, their length measured, and were dried at 70°C until they reached a constant weight. We used the resulting height-to-biomass regression to estimate standing cordgrass biomass in each plot. We also counted all juvenile (< 0.5 cm in diameter) and adult fiddler crab burrows at both the beginning and end of the experiment, because these organisms are known to influence cordgrass growth by oxygenating the sediment through burrowing (Bertness 1985, Daleo et al. 2007, Angelini & Silliman 2012, Gittman & Keller 2013, Raposa et al. 2018).

Infected and uninfected snails within each plot were counted twice weekly and replaced as necessary to maintain the assigned snail density and infection prevalence treatments for the 3-month duration of the experiment. During monitoring, any predatory mud crabs found within plots were removed and their burrows plugged with marsh sediment to discourage successful re-occupation.

We took final metrics of marsh vegetation characteristics in September 2016, 12 weeks after the beginning of the experiment. All snails were removed and dissected to confirm infection status. Because snail grazing had dramatically reduced stem densities in many plots, we were able to measure all stems within each plot to generate final plot biomass estimates by calculating and summing individual biomass estimates. Belowground

biomass cores (15-cm diameter x 25-cm height) were also taken from the center of plots. Cores were washed and root material separated from rhizomes. Roots and rhizomes were dried to a constant weight at 70°C and weighed.

The possible influence of caging artifacts on marsh invertebrates and cordgrass growth was assessed using paired t-tests. Specifically, we compared the number of total fiddler crab burrows, final stem density, initial aboveground biomass, final aboveground biomass, change in aboveground biomass, and number of flowering stems between cage controls and open controls.

Because fiddler crabs can positively influence cordgrass growth (Bertness 1985, Gittman & Keller 2013), we examined the relationship between burrow density and cordgrass stem density using a linear model. We validated model fit by examining model residuals, their distribution relative to fitted values, and normal Q-Q plots (*car* package, Chambers and Hastie 1992).

In accordance with our hypotheses, models including the interaction between parasite infection (uninfected versus infected) and snail density (20, 40, 50, 60, 70, 80, 90, or 100 snails per 0.5 m<sup>2</sup>) were fit for each response metric (belowground biomass, aboveground biomass, shoot density, and number of flowering stems). Additionally, all models initially included fiddler crab burrow density as a covariate. However, this covariate was ultimately not significant for any model, and was therefore dropped and each model re-run to include only the interaction term. We analyzed the interactive effects of infection status and snail density on belowground biomass using a two-way analysis of variance (ANOVA), with data log-transformed prior to analysis to meet model assumptions. Change in aboveground biomass was analyzed with a linear model, with initial aboveground biomass values for each plot subtracted from corresponding final values. Model assumptions were verified through assessments of homogeneity of variance (Levene's test,  $P > 0.05$ ) and examination of fitted residuals and normal Q-Q plots. The number of cordgrass inflorescences was modeled with a negative binomial generalized linear model (*glmmTMB*, Brooks et al. 2017). Model appropriateness and fit were confirmed through examination of simulated scaled residuals (*DHARMA*, Hartig 2022).

For each response metric, the significance of the interaction model was examined in an Analysis of Deviance Table using Wald chi-square tests (*car* package, Chambers & Hastie 1992). For all models, Tukey's post-hoc comparisons were used to assess pairwise differences for any significant treatment or interactive effects in the models (*emmeans* package, Lenth et al. 2021). All analyses were performed in the R statistical computing environment (v. 4.1.3; R Core Team 2018).

## Results

Initial estimated plant biomass was not significantly different among treatments ( $P = 0.057$ , one-way ANOVA). Additionally, there were no significant differences in the densities of fiddler crab burrows, plot elevation, and porewater salinity among treatments ( $P > 0.6$ , one-way ANOVA, for all response variables). The final mean infection prevalence for each treatment did not differ from initial assigned conditions. No false negatives were observed when snails were dissected following the end of the experiment. In treatments where they had been added, the mean weekly deviation in snail density never exceeded 10% for any plot. Exogenous snails very rarely found their way into experimental plots and were removed during weekly snail counts (<1 snail per plot per week). Those that were discovered within plots were typically below the size threshold (shell height <10 mm) associated with active grazing (Silliman & Bertness 2002). On average, less than one mud crab per week was removed from caged snail exclusion controls.

Cages used in this study did not have any detectable effects on cordgrass growth or the abundance of resident fiddler crabs ( $P > 0.07$  for all t-tests, Table S1). Resident fiddler crab abundance tracked positively with cordgrass stem density, though the relationship was weak ( $F_{1,62} = 4.108$ ,  $P = 0.047$ , Table S2, Fig. S1). We found no effects of snail density ( $F_{1,7} = 1.367$ ,  $P = 0.241$ ) nor parasitism on cordgrass belowground biomass ( $F_{1,7} = 0.045$ ,  $P = 0.834$ , Fig. S2).

Infection status and densities of snails significantly interacted with one another to affect aboveground biomass changes ( $P = 0.037$ , Table S3). Aboveground growth was generally higher in plots with infected snails com-

pared to those with uninfected snails (infected:  $13 \text{ g} \pm 1.67$  [estimated marginal mean  $\pm$  standard error], uninfected:  $0.269 \pm 1.67$ ,  $P < 0.0001$ ), and plots with parasitized snails were able to sustain aboveground production at higher snail densities than those with uninfected snails (Fig. 1). On average, plots with uninfected snails began to experience decreases in aboveground biomass at 64 snails/0.5 m<sup>2</sup>, while net losses in aboveground biomass in plots with infected grazers began at densities of 84 snails/0.5 m<sup>2</sup> (Fig. 1). We also found that, unsurprisingly, plots with greater densities of snail grazers lost more aboveground biomass (or demonstrated a gain that was much smaller than in plots with lower snail densities) (Fig. 1). The point at which snail density and infection status interacted to alter aboveground biomass was 50 snails/0.5 m<sup>2</sup>. When marsh plots were stocked with fewer than 50 snails, similar levels of aboveground growth occurred, regardless of parasite infection. However, trends in aboveground biomass production diverged at snail densities of 50 (infected: 22.4 g [lower and upper 95% CIs, 18.61-26.2], uninfected: 12.1 g [8.33-15.9]), with plots containing uninfected snails maintaining higher amounts of aboveground biomass at every density greater than or equal to 50 snails.

Although the number of inflorescences appeared to differ according to the presence of parasitized snails (Table S4), post-hoc tests revealed no significant increases flowering in plots with infected snails ( $P = 1$ , Table S5). Plots with 20 snails had more flowering cordgrass stems than did plots with 50 ( $P = 0.035$ ), 60 ( $P = 0.02$ ), or 70 ( $P = 0.008$ , Table S5) snails. No other clear differences in quantity of inflorescences existed between levels of snail density (Fig. S2, Table S5). Because plots with high snail densities ([?]80 snails/0.5 m<sup>2</sup>) were highly denuded by the conclusion of the experiment, the number of inflorescences could not be determined for the highest snail density treatments (Table S5).

### Discussion

Our field manipulation of grazer host density and trematode parasite presence confirmed the findings of previous studies that *Parorchis acanthus* can protect foundational plants by generating a trait-mediated trophic cascade, and showed that the emergence of these ameliorating effects occurs at intermediate levels of grazer host density. Our results underscore the context-dependent nature of trophic facilitation by parasites and inform a more robust understanding of when and where parasitism may promote ecosystem resistance to overgrazing in this system.

At an average infection prevalence, the trait-mediated impacts of trematode parasitism on snail grazing increased the grazer density threshold at which there was a net loss of cordgrass aboveground biomass by nearly 25% (Fig. 1). Additionally, the ameliorating trait-mediated indirect effects of *P. acanthus* on marsh aboveground growth emerged at intermediate densities of hosts (50 snails/0.5 m<sup>2</sup> or 100 snails/m<sup>2</sup>). At low grazer host densities, parasite reduction of per-capita grazing rates did not translate to detectable increases in aboveground plant biomass, likely because the top-down impacts of these snails only begin to emerge at densities of 60–144 snails per m<sup>2</sup> (Silliman & Zieman 2001, Silliman & Bertness 2002). While we had predicted that at high snail densities, the negative impacts of snail grazing on cordgrass would overwhelm any positive impacts of parasite behavior modification at the chosen prevalence, we did not find evidence for this at the highest levels of snail density used in our experiment. Such a threshold density almost certainly does occur in nature (*Littoraria* densities within consumer fronts can be as high as 2000 snails/m<sup>2</sup>) but this threshold may be considerably higher than highest density of snails used in our experiment (100 snails/0.5 m<sup>2</sup> or 200 snails/m<sup>2</sup>).

While our results indicate that the ameliorating trait-mediated impacts of parasitism by *P. acanthus* are mediated by grazer host density, the particular density at which these parasites have the potential to positively impact marsh plants is likely highly variable. For instance, a previous study in this system revealed that parasitism by *P. acanthus* led to significant reductions in snail grazing that translated to cascading effects on aboveground biomass at 10% and 30% infection prevalence and snail densities of ~143 snails/m<sup>2</sup> (Morton & Silliman 2020). While we found linear relationships between snail density and grazing pressure in the present study, previous work has shown that this functional relationship can be linear (Silliman & Zieman 2001), logarithmic (Atkins et al. 2015), or exponential (Renzi & Silliman 2021), depending on the specific context. This variation is likely mediated by local differences in abiotic stress, nutrient regime, vege-

tation characteristics, predation risk, benthic productivity, snail size structure (Atkins et al. 2015), and the strength of positive species interactions that enhance cordgrass growth (Bertness & Miller 1984, Bertness 1985, Gittman & Keller 2013, Atkins et al. 2015, Renzi & Silliman 2021).

Previous investigations in this system found that trait-mediated reductions in the top-down impacts of grazers on cordgrass biomass by *P. acanthus* was roughly proportionate to the level of infection prevalence (Morton 2018, Morton & Silliman 2020). However, the magnitude of the effect of trematodes on per capita snail grazing may vary with host condition, environmental factors or host genetics (Leung et al. 2010, Thomas et al. 2011). Additionally, different parasite species may yield varying trait-mediated indirect effects depending on the mechanisms through which they impact host physiology and modify snail feeding. The trematode species used in this study, *P. acanthus*, was chosen for its relative abundance at marsh die-off areas within our study site, but there are at least four trematode species that infect *Littoraria* which can occur at varying prevalence and may have different effects on snails (Holliman 1961, Coil & Heard 1966, Heard 1968, 1970). As a result, the density threshold at which snails exert strong control over cordgrass growth may vary depending on the trematode component community.

Trematode infection prevalence in *Littoraria* shows great spatial variation at both local and regional scales (Rossiter 2013, Morton & Silliman 2020). While many of the specific processes that mediate infection prevalence in *Littoraria* have yet to be experimentally tested, snail size, spatial variation in definitive host (bird) density, and tidal flooding regime, appear to be important determinants (Morton & Silliman 2020). Snail density itself may mediate infection dynamics in the field. Large densities of grazer hosts could result in lower individual encounter rates with mobile trematode miracidium, diluting infection risk and depressing prevalence (Mooring & Hart 1992, Buck & Lutterschmidt 2017). To date, observational and manipulative studies in this system have examined both parasite infection dynamics and parasite trait-mediated indirect effects across a fairly narrow range of host densities (Morton & Silliman 2020). Examining trematode infection dynamics across a wider range of *Littoraria* densities is necessary to determine whether dilution effects mediate snail infection at high densities.

The effects of both grazer density and parasitism on aboveground production were clear from our field experiment, but we detected no effect of either of these factors on cordgrass root or rhizome biomass (Fig. S2). Belowground growth of marsh plants can be affected through direct consumption by herbivores, including snow geese (Smith & Odum 1981) and burrowing crabs (Coverdale et al. 2012, Gittman & Keller 2013, Daleo et al. 2015). While *Littoraria* does not directly graze on belowground plant tissues, snail grazing could have indirect impacts on cordgrass belowground biomass through wholesale destruction of cordgrass aboveground tissues. However, removal of cordgrass roots and rhizomes is largely mediated by processes of microbial decay that likely operate on timescales greater than the duration of our experiment (Benner et al. 1987, Blum 1993, Blum & Christian 2004). As a result, determining how grazers and their parasites mediate cordgrass belowground biomass requires future investigation.

Parasite alteration of host behavior, whether it be manipulation, an antiparasitic tactic of the host, or merely a byproduct of infection, is likely common, though we still know little about how different parasites affect their hosts—even ecologically influential ones (Poulin et al. 1998, Morton 2018, Buck 2019). Additionally, the ecological reach of parasites through trait-mediated indirect effects is not reducible to the prevalence of behavior-altering parasites in a host population. Our results underscore the importance of host density as one determinant of the ecological reach of parasite-induced trait-mediated indirect effects. However, there are numerous factors that may ultimately influence such effects. Host populations, behaviors, and the environments in which those hosts exert influence through their behavior can vary widely in space and time. Fully incorporating parasites into our understanding of how ecosystems work necessitates that we not only quantify the often-subtle ways that parasites alter the behavior of hosts, but that we determine under what conditions these alterations can add up to have a wider ecological influence.

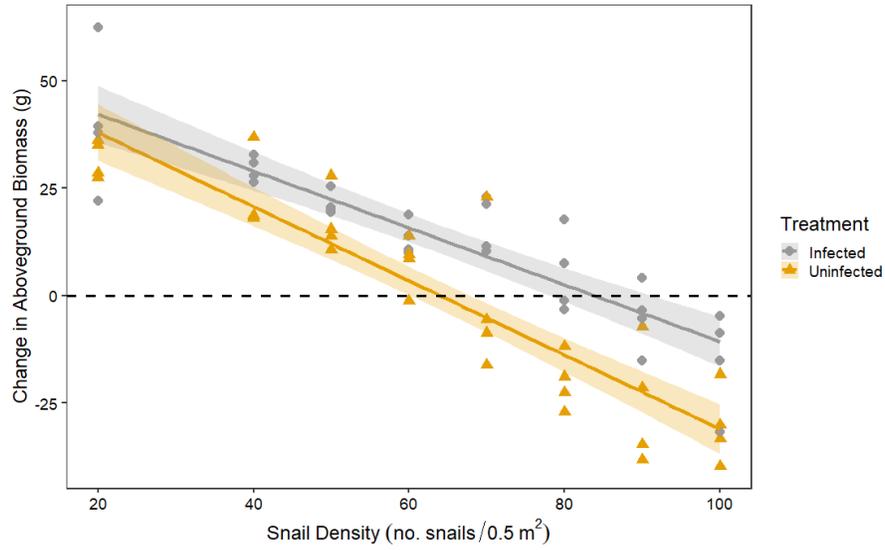
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Figures



**Figure 1:** Plot-level measurements of change in aboveground biomass according to parasite infection and snail density treatments. Dashed line at zero indicates no change in aboveground biomass, positive values indicate an increase in biomass during the study, and negative values indicate a loss in biomass. Lines depict modeled relationships, and associated shading represent 95% confidence intervals. The multiple  $R^2$  for this relationship was 0.83, with an associated correlation coefficient of 0.912.