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ORIGINAL PAPER

Biological control as an invasion process: disturbance and propagule pressure affect the invasion success of *Lythrum salicaria* biological control agents

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Abstract Understanding the mechanisms behind the successful colonization and establishment of introduced species is important for both preventing the invasion of unwanted species and improving release programs for biological control agents. However, it is often not possible to determine important introduction details, such as date, number of organisms, and introduction location when examining factors affecting invasion success. Here we use biological control introduction data to assess the role of propagule pressure, disturbance, and residence time on invasion success of four herbivorous insect species introduced for the control of the invasive wetland plant, *Lythrum salicaria*, in the Columbia River Estuary. Two sets of field surveys determined persistence at prior release sites, colonization of new sites, and abundance within colonized sites. We quantified propagule pressure in four ways to examine the effect of different measurements. These included three measurements of introduction size (proximity to introduction site, introduction size at a local scale, and introduction size at a regional scale) and one measure of introduction number (number of introduction events in a region). Disturbance was examined along a tidal inundation gradient (distance from river mouth) and as habitat (island or mainland). Statistical models and model averaging were used to determine which factors were driving invasion success. In this study we found: (1) sparse evidence for the positive influence of propagule pressure on invasion success; (2) disturbance can negatively affect the invasion success of herbivorous insects; (3) the effects of disturbance and propagule pressure are species specific and vary among invasion stages, and (4) not all measures of propagule pressure show the same results, therefore single measures and proxies should be used cautiously.

Keywords *Galerucella calmariensis* · *G. pusilla* · *Hylobius transversovittatus* · Introduced alien species · *Nanophyes marmoratus* · Purple loosestrife

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Introduction

Humans have spread organisms into new areas around the globe at an unprecedented rate, however, only a small proportion of these persist at introduction sites, colonize new sites, and proliferate at colonized sites to become successful invaders

(Mack et al. 2000). Understanding how introduced species respond at these three stages of invasion (Dawson et al. 2009) is important for directing management actions (Liebhold and Tobin 2008). Understanding invasion success is also useful for establishing desired non-native species. Some introductions, such as biological control agents, are intentional and invasion success is the desired effect. Understanding success during different invasion stages and within an environmental context can improve introduction methodology and agent selection.

Empirical evidence has shown a number of variables as being important for invasion success: propagule pressure of invader (Lockwood et al. 2005; Pemberton and Liu 2009), habitat disturbance or heterogeneity (Lozon and Maclsaac 1997), time since introduction (residence time; Pyšek and Jarošík 2005), distance of suitable sites to invasion foci (Rouget and Richardson 2003), and biological characteristics of the introduced species (Crawley et al. 1986; Pemberton and Liu 2009). Many studies have examined these variables individually, but few have studied multiple measures of propagule pressure, disturbance, and their interactions on invasion success (but see Britton-Simmons and Abbott 2008). In this study, we used statistical models to analyse data from intentional releases of four biological control agents in combination with data collected in two intensive field surveys to examine the interactive effects of propagule pressure, disturbance, and residence time on; (1) persistence at release sites, (2) colonization of new sites, and (3) abundance at colonized sites. To our knowledge no prior study has simultaneously examined the contribution of this number of variables and their interactions on the persistence and colonization of multiple introduced organisms.

Recent reviews have suggested invasion success can be primarily attributed to propagule pressure (Lockwood et al. 2005; Hayes and Barry 2008), especially during early stages such as persistence at introduction sites (Mikheyev et al. 2008) and colonization of new sites (Jeschke and Strayer 2006). Propagule pressure incorporates both the number of individuals released and the number of discrete release events (Lockwood et al. 2005); however, it is unclear how these combine to determine invasion success. How components of propagule pressure determine invasion success is also addressed as optimal release strategy theory in biological control (Shea and Possingham 2000) and should be more fully incorporated into general invasion theory. Although, larger populations are potentially more resistant to disturbance events and stochastic extinction (Lande 1993), there may be greater risk of a single large population going extinct than losing many small populations (Memmott et al. 1998; Liebhold and Tobin 2008). Memmott et al. (1998) found that many smaller introductions resulted in higher variability in establishment of gorse thrips (*Sericothrips staphylinuns*) yet also yielded a greater number of established populations, whereas, fewer large releases had lower establishment variation yet also lower potential number of establishments.

To what extent propagule pressure influences invasion is a long-standing (Beirne 1975) and unresolved question (Sax and Gaines 2008). The relative paucity of empirical tests of propagule pressure is due to limited knowledge of introduction size and number for most invasive species. A number of proxies have been used to examine propagule pressure, including: proximity to source (Edward et al. 2009), number of individuals in an isolated source population (Milton et al. 2007), genetic structure (Myburgh et al. 2007), historical records (Ruesink 2005), period of time over which species were regularly introduced (Pemberton and Liu 2009), relative frequency of potential introductions (Leung et al. 2004; Dehnen-Schmutz et al. 2007), number of broad locations where species were introduced (Jeschke and Strayer 2006), and number of offspring or propagules produced by the introduced species (Kolar and Lodge 2001). As many proxies for propagule pressure have been used, there is a need for studies to compare results using different measurements and scales of assessment.

Observational studies of factors affecting invasion success rarely have access to introduction information or are able to quantify invasion failures. Biological control programs provide a unique opportunity to study invasion processes because introduction information (location, time of release, and propagule pressure) is often recorded and releases can be manipulated to examine effects of propagule pressure on specific invasion processes (Beirne 1975; Grevstad 1999a, b; De Clerck-Floate and Wikeem 2009). Despite post-release monitoring of biological control species having multiple benefits, it is often neglected in biological control programs (Blossey 1995; Morin

et al. 2009). Monitoring of biological control programs provides information on early stages of spread and population growth which are rarely monitored for other introduced species (Fagan et al. 2002). Strategic releases based on experimental designs to assess invasion processes are rarely done (but see Grevstad 1999a; De Clerck-Floate and Wikeem 2009), therefore observational studies which examine existing releases are often the only way of utilizing biological control programs for this purpose. Observational studies may also facilitate examination over larger temporal and spatial scales than are possible for experimental studies.

Environmental heterogeneity and habitat disturbance have been shown to increase invasion success (Lozon and Maclsaac 1997). This effect is due to greater probability of finding suitable habitat for the introduced species in a heterogeneous environment (Melbourne et al. 2007) and disturbance, which reallocates formerly limiting resources, facilitating the colonization of newly arrived propagules (Lozon and Maclsaac 1997). However, few studies have looked at the interaction between propagule pressure and habitat disturbance (but see Britton-Simmons and Abbott 2008). Because most biological agents introduced for the control of invasive plants are monophagous, the colonization, establishment, and spread of the agent is strongly linked to the location and dynamics of the invasive host plant. This may cause complex relationships with disturbance because the effect of disturbance on the biological control agent may be a combination of that on the host species as well as the effect on the agent itself.

Residence time is a problematic variable in that it could have a positive, a negative, or a non-linear effect on invasion success (Groves 2006; Wilson et al. 2007). Colonization probability, spatial extent of an invasive species, and abundance are likely to be positively influenced by residence time (Wilson et al. 2007). However, probability of the persistence of an individual release is likely to be low in the early stages of colonization due to the influence of stochastic processes on small, and therefore vulnerable, populations (Lande 1993). Following this stage, a neutral or positive effect of residence time is likely as the populations grow or if populations nearby are able to re-invade the site. Finally, some invaders remain at low levels for many years (>50 years) before expanding their range and abundance (Groves 2006). Therefore, it is important to look at the effect of residence time during different stages of invasion and at different temporal scales.

In this study we examine the effect of multiple explanatory variables on the invasion of four biological control agents over a 10-year period and large spatial extent (128 km). In order to comprehensively test the effects of propagule pressure we examine both of its constituent parts, propagule size and number of introduction events. We use three measurements of propagule size; (1) number of organisms introduced at the nearest release site (local), (2) total number introduced within 10 km of survey site (regional), and (3) proximity of survey sites to nearest potential source and one measure of number of introductions; number of introductions within 10 km of survey site (regional) (Fig. 1). We examine the influence of disturbance along a 128 km gradient of inundation frequency and intensity (inundation regime) and between two inundation exposure intensities, low exposure associated with mainland habitats and high exposure associated with island habitats (hereafter referred to as habitat). Residence time is examined as years since introduction at either the release site or the nearest release site. We assessed three stages of invasion: persistence (presence of the agent at release sites), colonization (presence of agents at non-release sites), and abundance

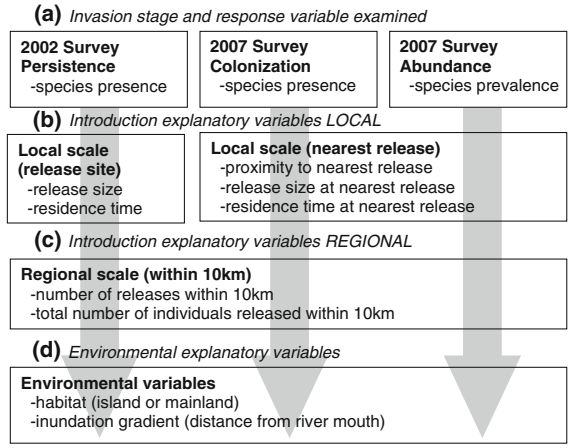

Fig. 1 Components of the study include; **a** the response variables at prior release sites and at newly colonized sites, **b** explanatory introduction variables at the local scale, **c** explanatory introduction variables at the regional scale, and **d** environmental variables. *Boxes* containing explanatory variables which lie directly below the invasion stage are used in the analysis for that invasion stage

(proportion of plants with evidence of agent presence at occupied sites).

We tested four hypotheses derived from theory and prior evidence. We expected (1) propagule pressure to be positively associated with invasion success, (2) propagule pressure to be more important during persistence and colonization stages than for abundance, (3) residence time to be positively associated with colonization success and abundance of the agents, whereas persistence to be high immediately after introduction and then decline due to stochastic extinction, and (4) we expected disturbance to differently affect the agents due to different feeding locations on the plant (i.e., different exposure to the environment).

Methods

Study system

Freshwater wetlands and riparian areas across temperate North America have been colonized by the invasive plant, purple loosestrife (*Lythrum salicaria*; hereafter loosestrife) (Blossey et al. 2001). These include freshwater habitats that experience a daily tidal amplitude >2 m along the Lower Columbia River Estuary (LCRE) in the Pacific Northwest USA. Loosestrife is a perennial herbaceous plant from Eurasia that has previously been shown to reduce the diversity of native plants (Schooler et al. 2006) and animals (Blossey et al. 2001; Schooler et al. 2009) in its introduced range. Dense stands of loosestrife have been observed on both islands and along the banks throughout the LCRE, from the freshwater tributaries near the river mouth to above the city of Portland, Oregon (136 km upriver).

A biological control research program was initiated in the 1980s (Malecki et al. 1993), resulting in four biological control agents being approved for use in controlling loosestrife; two leaf beetles (*Galerucella pusilla* Duftschmid; Coleoptera: Chrysomelidae and *G. calmariensis* L.), a root weevil (*Hylobius transversovittatus* Goeze; Coleoptera: Curculionidae), and a seed weevil (*Nanophyes marmoratus* Goeze; Coleoptera: Brentidae) (Malecki et al. 1993). The two leaf beetles are almost identical in morphology and occupy the same ecological niche (Blossey 1995) and can only be morphologically distinguished as adults (Piper et al. 2004). Therefore, *G. pusilla* and *G. calmariensis* (hereafter *Galerucella*) are analysed together in order to utilize damage effects as an indication of presence.

The different behaviours, feeding strategies, and reproductive capabilities of the insects may affect their ability to persist in the regularly inundated (tidal) habitats of the estuary. *Galerucella* adults actively drop from leaves when disturbed, whereas *N. marmoratus* adults remain in place, and *H. transversovittatus* adults actively cling to the plant (Schooler, pers. observation). In addition, *Galerucella* larvae are the most exposed as they feed on the outer surface of the leaves, while *N. marmoratus* larvae feed within the seed heads and *H. transversovittatus* larvae feed within the roots (Piper et al. 2004). *Galerucella* produce the most offspring (300–400 eggs/female, 1–2 generations/year), *N. marmoratus* produce fewer offspring (60–100 eggs/female, 1 generation/year) and *H. transversovittatus* produce more eggs per individual than *N. marmoratus* (150 eggs/female), but also have a longer generation time (1–2 years) (Piper et al. 2004).

The characteristic feeding behaviour of each insect allows assessment of its presence even when the adults are absent or difficult to find (i.e., *Galerucella* adults drop from the leaves and *H. transversovittatus* adults are nocturnal) and have been observed to remain on the plant throughout the season and in some cases on to the following season. *Galerucella* adults and larvae skeletonize leaves, *N. marmoratus* adults create small round "shot" holes in upper leaves and emerging adults leave holes in seed capsules, and *H. transversovittatus* adults characteristically remove the entire leaf edge in lower leaves, leaving a notch adjacent to the petiole, while larvae mine through the roots (Piper et al. 2004). In addition to feeding damage we include larvae and eggs in the survey method, which increases the detection of these agents when a single visit is made. *Galerucella* adults lay eggs daily throughout the breeding period (May to June and August to September) and these remain un-hatched on the leaves for 12 days, while *H. transversovittatus* larvae remain in the roots of the plant for up to 2 years (Piper et al. 2004).

Survey methods

Two surveys were conducted to measure the success of insect colonization in the estuary. In 2002, we

collected all biological control agent release records, mapped the location of releases made prior to 2002 and surveyed release sites for persistence of the insects. In 2007, we surveyed a portion of the estuary (25–75 km) to determine whether agents had colonized new sites and their relative abundance at these sites. Although all sites were visited once, we were able to increase the detection period by including presence of characteristic damage to the plants, eggs, larvae and adults. We then developed statistical models to determine the influence of environmental variables and release characteristics on the persistence, colonization, and abundance of agents throughout the estuary.

Data for loosestrife biological control agent releases were obtained from the Oregon Department of Agriculture and the Washington Department of Natural Resources databases including: date of release, coordinates of release site, species released, number of individuals released, and a detailed map of where each release was made within a loosestrife patch. Release records for the four biological control agents were mapped from first release through to 2006. All releases were made from regional field collections, rather than lab rearing, so provenance of insects was not expected to influence invasion success.

In 2002 (June–August), we surveyed each previous release site to look for signs that the population had persisted since release. Records are believed to be comprehensive as the state agencies responsible for biological control releases in the area follow the same reporting guidelines and they require local groups to submit release reports for all releases. Release locations were found using a GPS and maps. To determine biological control agent presence, each site was searched for adults, larvae, eggs, and/or the characteristic damage pattern for each insect for approximately 10 min by two researchers experienced in detecting the biological control agents in the LCRE. Several plants (5-10) were removed at each root weevil release site and roots were pulled apart to look for presence of larvae or larval damage. The presence of any one of the signs of occupation resulted in a "present" status.

In 2007 (May–June), we conducted surveys to determine colonization of new sites. We focused on loosestrife populations in tidal marshes in the mid-estuary region (river km 27–72). Survey sites were haphazardly selected on estuarine islands and the Oregon and Washington shoreline where herbaceous marsh vegetation was apparent. Two researchers searched each site for approximately 10 min. Number of plants inspected, and number of plants with signs (adults, larvae, eggs) or symptoms (characteristic feeding damage) of each biological control agent species were recorded. Where we found feeding damage characteristic of *H. transversovittatus* we excavated five plants and searched for larvae or larval galleries in the roots. As with the 2002 surveys, the presence of any one of the signs of occupation resulted in a "present" status for the new site. Abundance was calculated as the number of plants with damage from the biological control agents divided by the number of plants surveyed at each location. The location of each survey site was recorded using a GPS (Trimble Geo XT, Sunnyvale, CA). All locations were post-processed with Trimble Pathfinder Office (version 3.10) software (accurate to <1 m) and the nearest release site to each survey site was identified. Distance was measured to the nearest release site and to the mouth of the river using a GIS (ArcInfo 9.2, ESRI), and information on all release sites within a 10 km radius was recorded (number of releases, total number of individuals, earliest release).

We used four measures of propagule pressure: (1) proximity to introduction site, (2) introduction size at a local scale (nearest release), (3) introduction size at a regional scale (within 10 km) and (4) introduction number, the number of introduction events within 10 km. The regional scale using a 10 km radius was chosen based on previous research on dispersal and observations during this study. Both *Galerucella* and *N. marmoratus* were found at the most isolated sites available in this study (approximately 6 and 11 km from a release site, respectively). In addition, Albright et al. (2004) found that in a single season *Galerucella* had dispersed 9 km from the release site and Grevstad and Herzig (1997) found that *Galerucella* could locate and colonize loosestrife populations up to a kilometer away within a 7-day period. Ferrarese and Garono (2010) calculated that beetles could be passively transported in the bidirectional water flow in the LCRE by as much as 3.8 km upstream or 12 km downstream during one tidal exchange. They also found established *Galerucella* populations 3–5 km from known release sites. This was not the case for *H. transversovittatus* which did not disperse to any sites further than one kilometer.

We examined environmental disturbance in two general categories: habitat and inundation. Habitat was defined as island or mainland, where island sites are more exposed to tides and wind than mainland sites, and islands provide fewer places to retreat during the winter or extreme high tides and flood events. Frequency and duration of inundation is broadly related to distance from river mouth, as the tidal range (difference between high and low tide height) declines with increasing distance from river mouth (Fig. 2). Inundation gradient was standardized to values between zero and one by dividing the distance to the river mouth by the maximum distance then subtracting this value from one, therefore higher values are closer to the river mouth and have a higher inundation frequency and duration. All sites were in freshwater habitats above the influence of saltwater intrusion (Chawala et al. 2008).

Statistical model development

Two full models were developed for each response variable (colonization, abundance and persistence): one local model and one regional model. Persistence and colonization data were binary (presence or absence of agent) and were analyzed using generalized linear models (GLM) with binomial errors (Crawley 2005). Abundance data (proportion of sampled plants with signs of agents present) were arcsine transformed, and linear models were used (Crawley 2005). Colonization models only used locations which were non-release sites and abundance models were based only on the sites where the agent was present in the 2007 survey.

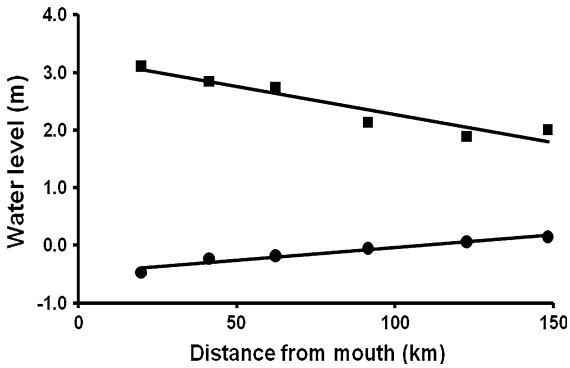

Fig. 2 Inundation regime in Lower Columbia River Estuary. Mean monthly high water levels (*squares*) are higher and mean monthly low water levels (*circles*) are lower for areas near the mouth of the Columbia River than areas upriver (data from river level gauges from July 2002 to June 2007)

In order to determine the most appropriate full models (containing all explanatory variables of interest) we assessed normality assumptions for residuals where necessary, looked at co-linearity among the explanatory variables, and tested for spatial autocorrelation between residuals for each response variable. Where necessary, variables were $\log_{10}$ transformed to ensure homoscedasticity of errors. We used variance inflation factors (VIF) (Zuur et al. 2009) to assess co-linearity between explanatory variables. Variables with a VIF > 3 were potentially co-linear with one or more other variables. Where this occurred, the variable with the highest VIF was removed and the analysis re-run on the remaining variables until all VIF's were less than three (Zuur et al. 2009). To assess spatial autocorrelation we used two methods: Moran's I for abundance data and Spline Correlograms for binary data (persistence and colonization models; Turner et al. 2001; Zuur et al. 2009). Correlograms were not used for assessing abundance data as they required a minimum of 50 data points (Turner et al. 2001) and the abundance data had 19 and 34 data points (*N. marmoratus* and *Galerucella*, respectively). Data to assess *Galerucella* persistence consisted of 15 data points, therefore we could not assess spatial autocorrelation for this data set. Spatial auto-correlation was assessed on the residuals from models which only included the intercept. Where spatial autocorrelation occurred we re-tested residuals for spatial autocorrelation from models with inundation gradient as the only explanatory variable, as this variable had a roughly linear spatial arrangement potentially accounting for the spatial autocorrelation.

Two environmental variables, habitat (island/mainland) and inundation gradient were included in all full models. The local models for colonization and abundance data included residence time, years since introduction at nearest release site, and two measures of propagule pressure: the number of individuals introduced at the nearest release site and proximity to the nearest release site (both $\log_{10}$ transformed). The local model for persistence used one measure of propagule pressure; number of introductions at the release site. Due to the small sample size for persistence data, no interactions were included in the full model and inundation was excluded from the regional scale model, as it was the least important in

the local model (see results). The regional models for all data sets included either number of individuals introduced within 10 km of a survey site or number of release events within 10 km of a survey site. As these two variables were co-linear (except in the persistence model) one was removed during VIF analysis. All explanatory variables were centred prior to analysis to improve the ease of interpreting model coefficients when interactions are present (Gelman and Hill 2007).

Following the methods described by Burnham and Anderson (2002), all possible candidate models for each response variable were compared using Akaike's information criterion (AIC). This allows models with different numbers of explanatory variables to be compared. We used a bias correction term for small sample sizes (AICc) (Burnham and Anderson 2002). The model with the smallest AICc value ($AICc_{min}$) was taken to be the best fitting model and all subsequent models were compared to $AICc_{min}$ to determine their relative support ($\Delta AICc_i = AICc_i - AICc_{min}$) and weighted using Akaike weights (w_i). As no $AICc_{min}$ models were clearly superior (large w_i relative to next best model) model averaging was performed (Burnham and Anderson 2002). Model averaging allows inference over a set of models rather than a single model. Model averaging was performed on the "top models", i.e., the minimum number of models with w_i summing to 0.95. The top models had a 95% likelihood of containing the best approximating model to the true model (Whittingham et al. 2005; Stokes and Cunningham 2006). A selection probability for each variable was calculated by summing weights for all top models with that variable present. Average parameter estimates (β) were calculated by multiplying the parameter estimate by the weight of each model, where missing variables were allocated a zero, and summing over all models. We calculated unconditional standard errors (not conditional on any particular model) for the entire set of candidate models using the conditional sampling variances and the weights for each model and generated upper and lower unconditional 95% confidence intervals for each variable. Parameter estimates from the full model were compared to model-averaged estimates to examine the potential impact of model selection bias (Burnham and Anderson 2002; Stokes and Cunningham 2006). Analysis was done using the R statistical program (R Development Core Team 2008) and the MuMIn library.

Results

The first releases were made in the estuary in 1997. From then through 2006 (inclusive), 130 releases were made in the estuary in which a total of 65,328 individual biological control agents were released. *Galerucella* had the largest release size, both in total (53,780) and prior to the 2002 persistence survey (17,550). *Galerucella* also had the largest number of release events in total (73) and equal to *H. transversovittatus* prior to 2002 (18; Table 1). The range of release sizes differed for each species; individual releases ranged from 60 to 600 for *N. marmoratus*, 50–208 for *H. transversovittatus* and 200–6,000 for *Galerucella*. These releases spanned the length of the estuary from the mouth of the Columbia River in Clatsop County (8 km) to the Rivergate District of Portland, Multnomah County (136 km).

Less than half of the potential model set was included in the set of top models (95% confidence

Table 1 Total number of release events and number of individuals released for *Galerucella spp.*, *N. marmoratus*, and *H. transversovittatus* in the Lower Columbia River Estuary

Species	Number of release events			Number of individuals released		
	1997–2002	2002–2007	Total	1997–2002	2002–2007	Total
Galerucella spp.	18	55	73	17,550	36,230	53,780
N. marmoratus	6	23	29	1,200	6,330	7,530
H. transversovittatus	18	10	28	1,718	1,700	3,418

Totals separated into two time periods; between the first release in 1997 and the June 2002 persistence survey and between the 2002 and May 2007 surveys

sets) for seven of the ten full models describing invasion success, indicating clear explanatory power for those variables included in the top models. In contrast the local and regional *Galerucella* persistence and regional *N. marmoratus* colonization models had a large percentage of the potential model set included in the top models (75, 63 and 69%, respectively), indicating the models for these response variables were poor (Stokes and Cunningham 2006). These response variables had a small potential model set (8, 8, and 13, respectively).

At least one measure of propagule pressure had a high selection probability (SP; >0.70) in four of the ten models and at least one measure of environmental variability had a high selection probability in six models, both with even splits between local and regional scale models. Residence time was the only variable, outside interaction terms, which had consistently low selection probabilities (≤0.28). Variables with selection probabilities ≥0.70 in one or more of the full models included proximity (2 out of 4 models), habitat (five out of ten models), inundation (five out of nine models, two confounded with spatial autocorrelation), number at nearest release (one out of four models), number of individuals introduced (one out of two models) and number of releases made (one out of four models) within 10 km. There was also high selection probabilities for two interactions: proximity to and number of individuals introduced at nearest release (one out of four models), and habitat and number of releases within 10 km (one out of three models). The selection probabilities for all variables in all full models are presented in Table 2 and the model averaging outputs in Table 3.

Persistence at release sites

Surveys of all 42 prior releases conducted in 2002 found that populations of the biological control agents persisted at 32 (76%) of the release sites. Signs of the agents were found at 10 of the 18 *Galerucella* release sites (56%), 17 of the 18 *H. transversovittatus* sites (94%), and 5 of the 6 *N. marmoratus* sites (83%). Due to the high persistence of *H. transversovittatus* and *N. marmoratus*, persistence models could not be developed for these two agents. There were insufficient degrees of freedom to include interactions in *Galerucella* persistence models and inundation (which had the lowest selection probability in the local model) was excluded from the regional model. Selection probability for measures of propagule pressure were low (≤0.47) and, interestingly, *Galerucella* populations did not persist at the sites with the two largest releases (3,000 and 6,000 individuals). Habitat was the only variable with a high selection probability (≥0.84) in either the local or regional models, although confidence intervals (CI) overlapped zero. Persistence of *Galerucella* was higher on mainland sites (five out of six persisted; 83%) than on island sites (two out of nine persisted; 22%). Number of release sites on islands varied with agent; there were nine *Galerucella*, two *H. transversovittatus*, and no *N. marmoratus* island release sites. Although *Galerucella* persistence was low on island sites, *H. transversovittatus* persisted at both of the island release sites.

Colonization of new sites

In 2007 we surveyed 52 loosestrife occupied sites from the mid-estuary region (27–72 km). Only non-release sites were used in colonization analyses and therefore the total number of non-release sites varied with agent, as nine of the survey sites were at prior *Galerucella* release sites, two were at *N. marmoratus* release sites, and one was a *H. transversovittatus* release site. Of the 52 sites in total, 36 (69%) had signs of the presence of one or more of the biological control agents.

Patterns of colonization differed for the four species. *Galerucella* had the highest colonization success (60%); followed by *N. marmoratus* (32%); and *H. transversovittatus*, which colonized only one site (2%), had the lowest colonization success. Due to low colonization of *H. transversovittatus* no models were produced for this species.

For *Galerucella* colonization models, inundation gradient accounted for spatial autocorrelation and was chosen in all top models; colonization probability increased with decreasing inundation intensity and frequency. No explanatory variables in the local *Galerucella* colonization model had a high selection probability (≤0.50). In the regional model, number of releases and habitat interacted (SP 0.71, CI's overlapped zero) to influence *Galerucella* colonization success. This interaction appeared to be driven by an outlier which had not been colonized and was surrounded by six releases. When this outlier was excluded the selection probability of this interaction

Table 2 Selection probability of each parameter for persistence, colonization and abundance models of *Galerucella spp.* and colonization and abundance models of *N. marmoratus*

Sp.	Scale	Invasion stage	P	N	Nr10	Ni10	H	I	R	P:H	P:N	P:I	H:N	N:I	H:Nr10	I:Nr10	H:Ni10	I:Ni10
Galerucella spp.	Local	Persistence	na	0.16	na	na	0.84	0.12	–	idf	idf	idf	idf	idf	na	na	na	na
		Colonization	0.50	0.33	na	na	0.40	1[a]	–	0.04	0.04	0.10	0.02	0.06	na	na	na	na
		Abundance	0.81	0.58	na	na	0.99	0.89	0.28	0.29	0.24	0.13	0.09	0.35	na	na	na	na
	Regional	Persistence	na	na	0.18	0.47	0.88	idf	–	na	na	na	na	na	idf	idf	idf	idf
		Colonization	na	na	0.78	VIF	0.78	1[a]	–	na	na	na	na	na	0.71	0.19	VIF	VIF
		Abundance	na	na	0.44	VIF	1	0.59	–	na	na	na	na	na	0.05	0.07	VIF	VIF
N. marmoratus	Local	Colonization	0.80	0.84	na	na	0.36	0.89	–	0.07	0.73	0.17	0.09	0.28	na	na	na	na
		Abundance	0.33	0.13	na	na	0.37	0.36	0.21	0.2	0	0.2	0	0	na	na	na	na
	Regional	Colonization	na	na	VIF	0.71	0.26	0.86	–	na	na	na	na	na	VIF	VIF	0	0.46
		Abundance	na	na	0.16	VIF	0.21	0.24	–	na	na	na	na	na	0	0	VIF	VIF

Selection probability is the sum of weights for each model that the specified parameter occurs in, therefore parameters with larger selection probabilities better explain the variation in the data. Parameters include: proximity to nearest release (*P*); release size at the nearest release (*N*), where the nearest release for the local persistence model was at the survey site; number of releases within 10 km (*Nr10*); number of individuals released within 10 km (*Ni10*); habitat (*H*); inundation (*I*); and residence time (*R*). Interactions between variables are represented by a colon separating the two parameters. Variables not present in full model were either due to non-applicability (*na*), dropped during variance inflation factor analysis (*VIF*), had insufficient degrees of freedom to include all applicable variables (*idf*), or parameters did not have enough variation to assess trends (–). Variables presented with a selection probability of zero were not present in the top 95% confidence set of models

[a] Confounded with spatial autocorrelation

decreased dramatically (SP 0.06) and number of releases within 10 km remained high (SP 1). Surprisingly, colonization success was consistently high in sites where there were less than twenty releases within 10 km and became more variable in areas of higher release density (Fig. 3). Although the interaction between inundation and number of releases had a low selection probability (0.19) it is possible that it explains much of this trend as areas of high density releases were clustered at either end of the inundation gradient. Therefore, variation within this group may be driven by inundation pressure rather than propagule size. There is a stronger trend toward greater colonization variation in sites with higher inundation scores (Fig. 3).

For the local *N. marmoratus* colonization model, inundation and an interaction between release size and proximity had high selection probabilities (0.89 and 0.73, respectively, CI's overlapped zero). Inundation had a negative effect on *N. marmoratus* colonization success, with little difference between island and mainland sites. For sites close to a release site, propagule size had an expected positive influence on colonization success, however, when sites were more remote there was a slightly negative trend (Fig. 4a). There was little difference between island and mainland trend lines, for simplicity the lines in Fig. 4a are for mainland sites. For the *N. marmoratus* regional model, release size within 10 km and inundation had high selection probabilities (0.71 and 0.86, respectively, CI overlapped zero) and both had a negative relationship with colonization success (Fig. 4b). Similar to the *Galerucella* colonization model, the interaction between inundation and the regional release size had a low selection probability (0.46). However, this may explain the unexpected pattern between propagule pressure and invasion success. All of the sites exposed to small regional release sizes (<1,200) were in the low inundation zone (inundation score <0.70), while areas with large regional release size were clustered at either end of the inundation gradient. The negative trend highlighted above was only for releases in the high inundation zone (Fig. 4b).

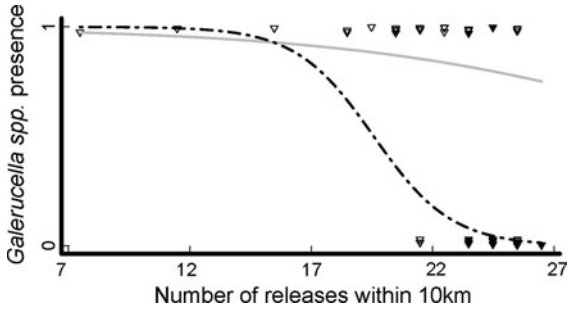

Fig. 3 Colonization success of *Galerucella* with number of releases within 10 km. Sites with high inundation values (>0.74) are represented by *solid triangles* and low inundation values (≤0.74) by *open triangles*. *Lines* are model averaged predictions taking into account other explanatory variables. *Lines* are plotted based on the model averaged coefficients, where inundation is set to its 1st (*gray line*) and 3rd (*black line*) quartile values, all other explanatory variables not graphed are set to their mean value

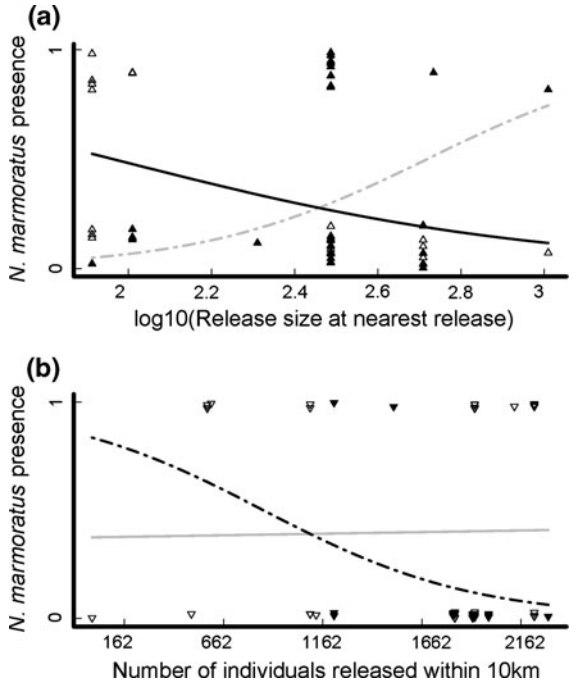

Fig. 4 Colonization success of *N. marmoratus* with **a** number of individuals released at the nearest release site and **b** number of releases within 10 km. Data points are divided by **a** distance (close sites < mean distance, *solid triangles* and far sites > mean distance, *open triangles*) and **b** inundation (high > 0.74, *solid triangles* and low ≤ 0.74, *open triangles*). *Lines* are model averaged predictions taking into account other explanatory variables and are based on model averaged coefficients, where parameters not graphed are set to their mean with the exception of **a** distance to the nearest release and **b** inundation, which are set to their 1st (*gray line*) and 3rd (*black line*) quartile values. *Lines* represent mainland sites only. Points are spaced vertically for clarity

Abundance at new sites

Abundance of agents at colonized sites ranged from 10 to 100% of surveyed plants exhibiting signs of the biological control agent. At 12 sites (33%) all plants showed signs of damage and at 26 sites (72%) over half the plants showed signs of agent presence. In order to examine the success at sites where the agent was present, models were developed for *Galerucella* and *N. marmoratus* with the same explanatory variables as for the colonization models. All variables in either of the *N. marmoratus* abundance models had low selection probability ($\leq$0.37). Habitat had the highest selection probability when predicting *Galerucella* abundance at both scales (SP $\geq$ 0.99, CI did not overlap zero). Consistent with persistence models, *Galerucella* abundance was higher on mainland sites (mean = 0.86, SE = 0.06) than island sites (mean = 0.49, SE = 0.08). In local models, inundation and proximity to nearest release also had high selection probabilities (0.89, 0.81, respectively, CI overlapped zero). Both inundation and distance to nearest release had a negative influence on abundance (Fig. 5).

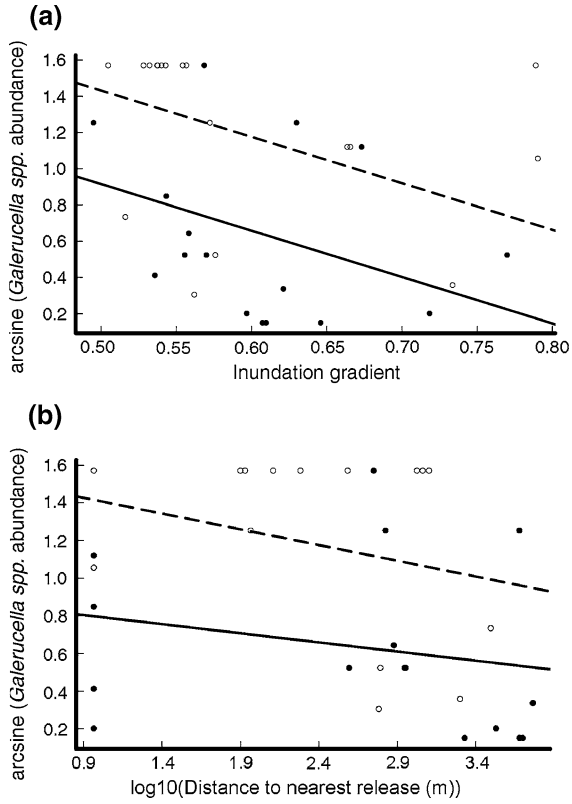

Fig. 5 Abundance of *Galerucella* at colonized sites. *Lines* are derived from model averaged coefficients. Abundance decreases with increasing **a** inundation intensity/frequency and **b** isolation from release sites. Mainland sites (*open circles*, *dashed line*) have a consistently higher abundance than island sites (*solid circles*, *solid line*)

Discussion

Prior studies have determined that propagule pressure is a strong determinant of invasion success (Lockwood et al. 2005; Hayes and Barry 2008; Pemberton and Liu 2009). However, our study found that it had limited and varying influence on invasion success, differing with species, invasion stage, and scale of assessment. Although five propagule pressure parameters had high selection probabilities (SP > 0.6) in four models, only one had a positive relationship with invasion success irrespective of other conditions and one was positive when the new site was close and negative when far from a release site. In contrast, three propagule pressure parameters with high selection probabilities had a neutral relationship with invasion success under certain conditions and a negative relationship under other conditions. In addition, the way we measure propagule pressure influenced the likelihood of it being detected as an important driver in invasion success. This is problematic as many alternative methods of measuring propagule pressure have been used to overcome the lack of introduction information (e.g., Jeschke and Strayer 2006; Milton et al. 2007; Mikheyev et al. 2008), with differences found in the effect of propagule pressure perhaps due to differences in the measure used. Chytrý et al. (2008) suggest more accurate measures of propagule pressure are needed and proxies may not identify an important effect. Biological control programs with specific introduction information are useful in examining the direct influence of propagule pressure; the variable influence at different spatial scales and the accuracy of propagule pressure proxies.

We also found that propagule pressure varied in importance at different spatial scales. The agents with the highest release size and number (*Galerucella*) had the highest colonization success and abundance; however, they also had the highest variation in persistence. When assessing the importance of

propagule pressure at finer scales models containing propagule pressure had high probabilities of being selected and a positive trend with invasion success in the colonization stage for one species and the population increase stage for the other. If the regional propagule pool is large, as it is for *Galerucella*, the influence of local propagule variation may be undetectable (Hylander 2009). However, this is unlikely to explain the low importance of propagule pressure in *Galerucella* persistence models, as similarly low selection probabilities occurred for *N. marmoratus,* which had a much smaller overall release size. Similarly, propagule pressure may only have a positive trend when introduction sizes are below a certain threshold and increases above that threshold have no further effect. This also is unlikely to explain the patterns in *Galerucella* persistence models as only 33% of release sites started with ≥540 individuals, a release size that a prior study found resulted in 100% establishment (Grevstad 1999a). These results support findings by Pyšek et al. (2008), where different explanatory variables explain invasion success at different spatial scales.

Propagule pressure was only important, with a positive effect on success, during the colonization stage for *Galerucella* and the population increase stage for *N. marmoratus*. Many studies examining the role of propagule pressure look at only one invasion stage (e.g., Ruesink 2005; Hylander 2009) and therefore may be missing its importance, or lack of importance, in other stages. Contrary to our findings, Mikheyev et al. (2008) found that relative frequency of introductions increased the persistence of fire ant (*Wasmannia auropunctata*) populations at introduction sites but not the colonization of new sites. Pyšek et al. (2008) suggests early stages of invasion are more likely to be influenced by human-increased propagule pressure, whereas later stages of invasion are controlled by the biological traits of the invader. This may explain the high abundance of *Galerucella*, which has higher fecundity than the other two introduced species (Piper et al. 2004). Using biological control programs to assess early stages of invasion may provide important information on the role human-mediated propagule pressure plays in initial invasion success.

The high persistence of *H. transversovittatus* and *N. marmoratus* at release sites may be due to release location or agent behaviour and larval location (protected within roots and flower buds, respectively). Prior to 2002, no island releases were made for *N. marmoratus*, while there were only two island releases made for *H. transversovittatus.* However, this is unlikely to explain high persistence as *H. transversovittatus* persisted at both island releases (high exposure sites) and neither *N. marmoratus* colonization nor abundance was highly influenced by habitat. High persistence may also be influenced by avoidance of enemies (Williamson and Fitter 1996) as these two species spend part of their lives within the plant tissue (Piper et al. 2004).

Although disturbance is often associated with successful invasion (Lozon and Maclsaac 1997), we found that loosestrife biological control agents were often negatively associated with disturbance along an inundation gradient and disturbance associated with high exposure to disturbance, on islands, within the LCRE. This relationship is unlikely to reflect a negative influence of disturbance on the host plant as loosestrife forms dense stands along the entire reach of the LCRE and along both island and mainland shorelines. The influence of disturbance is therefore more likely to be a direct affect on the insects themselves through dislodgment (Ferrarese and Garono 2010). Mainland sites may provide more refuge opportunities for overwintering insects to retreat from inundation, thus allowing populations to persist and reach higher abundance than island sites. Mainland areas may also maintain source populations in higher elevation areas with fewer inundation events and therefore reduce localized extinction. Tidal inundation, as estimated by distance to river mouth, had negative effects on colonization of agents. Denoth and Myers (2005) suggested the low persistence of *G. calmariensis* in estuarine environments may be linked to hydrologic regime. These negative relationships support the conclusion by Lozon and Maclsaac (1997) that plant invasions are more frequently associated with environmental variability for their establishment and range expansion than animals.

Environmental disturbance may disrupt the effect of propagule pressure. Although this study examined the influence of propagule pressure over a disturbance gradient, the entire study was conducted within an estuary. The survey sites sampled in this study are likely to be exposed to more frequent and more intense disturbance events than most non-estuarine wetlands. Previous research in non-estuarine

wetlands detected a clear effect of propagule pressure on *Galerucella spp*. establishment and population growth rate (Grevstad 1999a). Therefore, the limited support for propagule pressure as a driver for invasion success found in this study may be due to the overwhelming influence of disturbance.

This study found no support for invasion success varying with residence time. Residence time is a difficult variable to assess as introduced species may persist at low numbers at an introduction site for a long time before conditions are ideal for expansion in size and range (Groves 2006; Wilson et al. 2007). Although this study encompassed a number of years, this may not have been enough time to assess the influence of residence time on invasion success.

Biological control programs are useful for examining invasion processes as they provide detailed information on the introduction of exotic species into a new area. However, the release sizes and locations made in this study were not designed to examine the effects of disturbance and propagule pressure and this makes statistical analysis and interpretation more challenging. For example, clustering of large releases and large number of releases at either end of the inundation gradient may explain unexpected negative relationships between colonization and propagule pressure at the regional scale. In addition, one model found an unexpected relationship between propagule size and *N. marmoratus* colonization success, where there was a slight negative trend when survey sites were further from release sites. This may be due to the diminished influence of the release site at more remote locations and the colonization success may be driven by variables not examined in this paper. Therefore, biological control agent releases should be made with consistent variation in release size through space and time to assess the influence of propagule pressure on invasion success. Although release programs specifically designed to assess invasion processes can avoid confounding variables, post-release assessments like this one may better reflect the process of un-intentional invasions, which are of interest to managers of invasive species.

Biological control programs can improve probability of success by planning releases based on how introduction effort and environmental variables affect agent colonization and establishment. We found that biological control agents responded differently to the environments in the estuary and varied in success during different invasion stages, suggesting that it is unlikely that a single species will be able to successfully control loosestrife throughout the estuary. Both *N. marmoratus* and *H. transversovittatus* have high persistence irrespective of environmental variability or release size. Therefore, they should be released in low numbers throughout the estuary with a particular focus on islands, where *Galerucella* have poor persistence. Since both *N. marmoratus* and *Galerucella* are able to colonize loosestrife populations >6 km from release sites, these agents require fewer release locations than *H. transversovittatus*, which exhibits poor dispersal and colonization ability. As inundation negatively effects colonization success, but has a lower likelihood of influence on persistence and abundance of *N. marmoratus* and persistence of *Galerucella*, a greater number of releases near the mouth of the estuary will be beneficial for more rapid spread.

Previous studies have highlighted the possibility and the problems associated with false zeros in observational studies (Martin et al. 2005) and this was considered in this study due to the short sampling period. Martin et al. (2005) suggest false zeros can arise from two sources; (1) sampling a small spatial or temporal area relative to that experienced by the study organism and which is therefore not present at the place and time of survey and (2) inability to detect a species when it is present due to its cryptic nature. By using signs and symptoms of agent presence that persist at a site for long periods, we are able to reduce the likelihood of false zeros due to the first source of detection failure. The second source is also unlikely to influence our results as, although the adults of the four focal species may be cryptic (*Galerucella* adults drop from the leaves and *H. transversovittatus* adults are nocturnal), their feeding damage and eggs are less so. Detection probability is also unlikely to vary with disturbance intensity as eggs, larvae, and damage are unlikely to be affected by inundation (Garono, unpublished data).

The results from this study indicate: (1) there is little evidence for the role of propagule pressure in invasion success of the examined herbivorous insects; (2) disturbance can negatively affect the invasion success of herbivorous insects; (3) the effects of disturbance and propagule pressure are species specific and vary among invasion stages, and (4) not all measures of propagule pressure show the same

results, therefore single measures and proxies should be used cautiously. We demonstrate that analysis of prior biological control releases can be useful to both better understand the processes of invasions and to improve biological control programs.

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Appendix

See Table 3.

Table 3 Model averaging output for all variables present in the top model selection

Variable	β	Variance	SE	USE	LCI	UCI
Galerucella spp./persistence/local						
Intercept (*is.*)	−1.06	0.622	0.883	0.957	−2.93	0.818
H (*main.*)	1.3	8.672	2.533	2.717	−4.02	6.628
Nr	0.060	0.073	0.235	0.254	−0.437	0.558
I	−0.173	3.36	0.707	0.759	−1.66	1.31
Galerucella spp./persistence/regional						
Intercept (*is.*)	−1.29	1.03	0.994	1.08	−3.42	0.834
H (*main.*)	2.07	54.93	3.424	3.7	−5.2	9.334
N10	<−0.001	<0.001	<0.001	<0.001	−0.001	<0.001
NR10	0.581	57.6	1.51	1.58	−2.52	3.69
Galerucella spp./colonization/local						
Intercept (*is.*)	0.619	0.152	0.598	0.613	−0.583	1.82
P (*is.*)	−0.647	1.46	1.01	1.03	−2.66	1.37
H (*main.*)	0.175	0.788	1.371	1.397	−2.563	2.91
N (*is.*)	0.724	48.1	1.93	1.98	−3.15	4.6
R	−17.0	1030	5.6	5.77	−28.3	−5.7
P:H (*main.*)	−0.647	0.099	0.117	0.121	−0.238	0.238
P:N	0.005	8.64	1.249	1.277	−3.138	1.859
P:I	0.515	2140	2.6	2.67	−4.72	5.75
H:N (*main.*)	0.654	1.9	0.234	0.239	−0.538	0.398
N:I	−0.883	6108.1	4.93	5.04	−10.03	9.71
Galerucella spp./colonization/regional						
Intercept (*is.*)	3.35	88.5	3.01	3.06	−2.66	9.35
H (*main.*)	1	167.3	5.94	6.05	−10.87	12.85
NR10 (*is.*)	−0.847	0.348	0.756	0.769	−2.36	0.661
I	−8.68	933	5.4	5.51	−19.5	2.11
H:NR10 (*main.*)	0.002	0.818	1.569	1.596	−3.132	3.131
NR10:I	−1.18	21.1	1.9	1.92	−4.94	2.59
Galerucella spp./abundance/local						
Intercept (*is.*)	0.659	<0.001	0.118	0.123	0.418	0.899
P (*is.*)	−0.097	<0.001	0.106	0.109	−0.31	0.116
H (*main.*)	1.176	<0.001	0.285	0.296	0.595	1.756

Table 3 continued

Variable	β	Variance	SE	USE	LCI	UCI
N (*is.*)	0.425	0.143	0.571	0.581	−0.714	1.56
I	−2.56	4.42	1.37	1.41	−5.32	0.207
R	−0.018	<0.001	0.036	0.036	−0.089	0.053
P:H (*main.*)	−0.167	<0.001	0.226	0.23	−0.618	0.284
P:N	0.179	0.023	0.308	0.311	−0.43	0.788
P:I	−0.09	0.036	0.23	0.235	−0.551	0.371
H:N (*main.*)	0.477	0.153	0.709	0.722	−0.938	1.888
N:I	3.7	1210	5.41	5.46	−7	14.4
Galerucella spp./abundance/regional						
Intercept (*is.*)	0.617	<0.001	0.114	0.118	0.385	0.849
H (*main.*)	1.234	0.001	0.271	0.281	0.682	1.786
NR10 *(is.)*	−0.01	<0.001	0.016	0.016	−0.042	0.021
I	−0.978	1.6	1.11	1.13	−3.19	1.24
H:NR10 (*main.*)	−0.01	<0.001	0.018	0.019	−0.046	0.027
NR10:I	0.021	<0.001	0.051	0.052	−0.08	0.123
N. marmorattus/colonization/local						
Intercept (*is.*)	−1.2	0.086	0.536	0.548	−2.27	−0.125
P (*is.*)	0.44	1.25	0.988	1.01	−1.54	2.42
H (*main.*)	−1.034	0.141	0.92	0.939	−2.87	0.808
N (*is.*)	0.979	11.2	1.78	1.81	−2.57	4.53
I	−9.2	1320	5.9	6.01	−21	2.58
P:H (*main.*)	0.576	1.505	1.3	1.325	−2.021	3.173
P:N	−9.94	3690	7.65	7.74	−25.1	5.24
P:I	2	5780	5.19	5.26	−8.31	12.3
H:N (*main.*)	1.248	13.18	2.37	2.405	−3.467	5.97
N:I	−4.47	10600	8.16	8.24	−20.6	11.7
N. marmorattus/colonization/regional						
Intercept (*is.*)	−0.965	0.043	0.452	0.462	−1.87	−0.059
H (*main.*)	−0.857	0.066	0.725	0.739	−2.306	0.592
N10	−0.001	<0.001	0.001	0.001	−0.002	0.001
I	−5.56	465	4.6	4.7	−14.8	3.64
N10:I	−0.01	<0.001	0.013	0.013	−0.035	0.015
N. marmorattus/abundance/local						
Intercept (*is.*)	0.373	<0.001	0.129	0.137	0.105	0.641
P (*is.*)	−0.206	0.033	0.337	0.34	−0.872	0.46
H (*main.*)	0.343	0.002	0.259	0.271	−0.189	0.874
N	0.007	<0.001	0.051	0.054	−0.099	0.113
I	−0.76	4	1.22	1.24	−3.2	1.68
R	−0.017	<0.001	0.036	0.037	−0.089	0.056
P:H (*main.*)	0.099	0.196	0.837	0.842	−1.551	1.75
P:I	1.91	247	3.12	3.14	−4.23	8.06
N. marmorattus/abundance/regional						
Intercept (*is.*)	0.342	<0.001	0.115	0.122	0.102	0.582
H (*main.*)	0.378	<0.001	0.194	0.204	−0.023	0.778

Table 3 continued

Variable	β	Variance	SE	USE	LCI	UCI
NR10	−0.003	<0.001	0.011	0.012	−0.026	0.021
I	−0.257	0.451	0.578	0.6	−1.43	0.918

β average parameter estimates, variance, *SE* standard error, *USE*unconditional SE, *LCI* lower confidence interval, *UCI* upper confidence interval for each model (defined by species/invasion stage/scale). Intercept and slope (when habitat is present in an interaction) *is.* is for island and *main.* mainland separately

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