Effect of invasive plants on herbivores and herbivory preferences

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Invasive species are one of the top worldwide threats to native biodiversity (Wilcove et. al 1998). As defined by the IUCN (International Union for Conservation of Nature), invasive species are "plants, animals or other organisms introduced by man into places out of the natural range of distribution, where they become established and disperse, generating a negative impact on the local ecosystem and species". They can spread by water, wind, animal and/or human activities (Tallamy 2004).

Invasive plants were brought by humans primarily for the purpose of having insect resistant ornamentals (Tallamy 2004). Invasive eradication can be successful at small scales (Flory 2010), but large scale removals are more complex.

With the introduction of exotic plants comes the potential that they may adapt and evolve within their new environment and therefore, expand their population (Miller and Matlack 2010). For example, exotic plants may escape herbivory pressure in their new environments that native plants are susceptible to (enemy release hypothesis) (Liu et. al 2007) and evolve via local selective pressures (Mooney and Cleland 2001). On the other hand, native organisms hinder the success of an invasion of exotic organisms through biotic resistance (Maron and Vila 2001).

The introduction of non-native plants can have a negative effect on the natural flora by outcompeting native plants, reducing plant diversity, and shifting species composition towards non-native dominated habitats. Plant invasion can also shift insect interaction. Exotic plants can affect herbivores abundance and therefore their predators abundance (Tallamy 2004). Eventhough herbivores may feed less on this new source because of the lack of co-evolved relationship (Liu and Stilling 2006). This does not mean that they aren't going to gain new enemies in this new environment. Exotic generalist herbivores can be their new enemies in this new environment. Studies have shown, in general, specialist native herbivores prefer native plants (Tallamy 2004) while generalist herbivores are more willing to feed on exotic plants species than are specialists (Morrison and Hay 2011, Keane and Crowley 2002). Also, exotic plants may escape specialist predators from their natural environment, so that herbivory from specialists in their new environment will be weak (Levine et. al 2004).

Because of the explanation previously discussed native plants will be more susceptible of being suppressed by herbivores than exotic plants (Hill and Kotanen 2009; reviewed by Morrison and Hay 2011). Eventhough native plants are a limiting foodsource they can be the preferred fooodsource. Therefore, indigenous plants will be more affected because there will be more generalists and specialists feeding and damaging native plants compared to exotic plants. The increasing number of generalists invading the area has a suppressing effect on native plants, inhibiting the healthy growth of their population and affecting their fecundity (Tallamy 2004) but invasive plants can benefit them by having an unlimiting foodsource and increasing species abundance and therefore, species richness of herbivores that feed on invasive plants may increase with in invaded areas (Brändle et. al 2008). This increased can be caused by the lack of native food sources and the abundance of the introduced food source and tendency of some herbivores to feed on the most encountered food source. For example, a recent showed that as the invasive plant *Medicago* increased, the number of herbivores in the genus *Hypera* and predatory spiders also increased (Lau 2012). But it was also found that there was no significant difference in densities of spiders in invaded versus un-invaded areas, suggesting that spiders are feeding on the food source that is nearest and available to them (Lau 2012). However this study was performed during the months where the spiders were more abundant, suggesting that they are tracking food availability and therefore, an increase of spider abundance doesn't necessarily mean a positive effect.

Another example was a study performed with deer mice (*Peromyscus maniculatus*) (Ortega et. al 2004). They found increased deer mice populations in grasslands with high densities of an invasive knapweed (*Centaurea maculosa*) and gall fly (*Urophora* spp.) which were used as food sources compared with those where the native vegetation dominated, but this was only for a short period of time (Ortega et. al 2004). Although their study suggested a positive initial effect, the breeding productivity decreased during the summer because of the lack of gall flies in the invaded areas, meaning a decrease in population size of deer mice in these habitats (Ortega et. al 2004).

I hypothesize that sites dominated by invasive plants will have higher species richness and relative abundance of herbivores than sites dominated by native plants. This is because generalist herbivores are more likely to consume invasive plants than specialist herbivores. Conversely, I hypothesize that sites dominated by native plants will have lower species richness and relative abundance of herbivores than sites dominated by the invasive species due to their shared co-evolutionary history. I hypothesized that there will be less herbivory overall in sites dominated by invasive species of plants than in the sites dominated by native plants.

When selected invasive plant species are experimentally removed and introduced, I expect to see a decrease of herbivores. Therefore I expect to see an increase in herbivory. I also expect to see more predators at native sites than at invaded sites.

Materials and Methods

Linaria dalmatica (Dalmatian toadflax) is one of the most common invasive species throughout the National Bison Range (Pauline Prarie). *Linaria dalmatica* was introduced in North America as an ornamental plant in the 1800's from Eurasia. Its native habitat extends from central Europe to Central Asia. *Linaria dalmatica* also has medicinal uses and as fabric die. Dalmatian toadflax grows in its invasive range in poor terrains and mixed prairie (Wilson et. al 2005).

Field Sampling

Invaded Vs. Un-invaded

To look at the effects of the invasive plant *L. dalmatica* on richness and abundance of herbivores, I sampled areas that were dominated by *L. dalmatica* and areas that where uninvaded by *L. dalmatica* with similar characteristics. I used two linear transects from 20m to 30m, smaller ones were fit to accommodate similar characteristics than the others. The 20 m one had fewer quedrants which were accommodated every 5m apart.there was 10 sites in total which 5 were invaded with L. dalmatica and 5 had native plants which predominately were *Erigeron bellidiastrum.* . Every 5m along the transects, we set up a permanent $0.625m^2$ quadrant by marking the corners with flagging. To estimate *L. dalmatica* densities, we counted all individuals of *L. dalmatica* in each quadrant. Invaded sites with *L. dalmatica* ranged from 79 to 152 individuals on the $0.625m^2$ and the native sites ranged from 22 to 54 individuals per each $0.625m^2$.

Predator abundance and Herbivore abundance

To measure the influence of *L. dalmatica* on the abundance and richness of herbivores and their invertebrate predators, I sampled invertebrates at each site. I placed 6 pitfall traps in each of the ten sites to measure abundance and species richness of ground dwelling arthropods, especially spiders. Plastic cups (16oz.) were used as pitfall traps and sunk into the ground every 10 m along each transect. The pitfalls were left for two days and then collections preformed each day for two weeks. Arthropods were sorted and identified to family.

Herbivores on invaded and un-invaded sites were sampled using the sweep net method. We used 125 sweeps per transect (5 sets of 25 sweeps). Insects were stored in plastic Ziploc bags (one gallon), and identified by family. Invertebrates were collected weekly for 2 weeks.

Herbivory rate

To measure herbivory in invaded and uninvaded sites, I sampled herbivore damage in the $0.625m^2$ quadrats. A meter stick was laid across each $0.625m^2$ quadrant, and one leaf was examined for signs of herbivory every 5cm along the meter stick. I classified the herbivory as mammalian or insect. This allowed me to measure the herbivory in each plot. This monitoring will be repeated for two weeks.

Experimental removals and introductions

I set up 6 additional sites where the invasive plant *L. dalmatica* was dominant. These sites ranged from 44 to 159 individuals per $0.625m^2$. Each site was monitored as described above. After the first sampling session, experimental removals and introductions of plants were conducted and then the sites were sampled again after one week.

For the experimental removals (three sites), I clipped all *L. dalmatica* in every $0.625m^2$ quadrat in each transects. For the experimental introduction (three sites), I introduced three *Erigeron bellidiastrum* plants (a native species) in flower pots in each quadrant. At each of these 6 sites, I monitored herbivore abundance, predator abundance and herbivory rate as described above to determine if adding native plants or removing invasive plants alters the herbivore and predator communities.

Statistical analyses

For comparing herbivory rates between native and invasive sites I used a t-test. To compare herbivory rate between all sites I used repeated measures analyses of variance (ANOVA). Also I used repeated measures ANOVA to compare arthropod abundance and richness among treatments and sites. Statistics were run using SYSTAT 13.

Results

Herbivory rates

There was no significant difference between the total herbivory in invaded versus native sites (t=1.35, df= 1.80, P =0.19; Figure 1a). However, differences were observed when evaluating herbivory by mammals and insects separatelyMammalian herbivory was greater in native sites (t= 7.62, df=1.80, P < 0.01; Figure 1b, while insect herbivory was greater on invaded sites (t=5.35, df=1.80, P=0.000043; Figure 1c).

A similar pattern was observed in the plots with experimental introductions and removals. There was no difference in total herbivory among sites ($F_{3,24}$:2.37, P=0.095; Figure 2a), time (week) ($F_{1,24}$:2.99, P=0.097; Figure 2a), or the interaction term ($F_{3,24}$:1.19, P=0.33; Figure 2a). When braking apart the total herbivory among the four different sites we found that mammalian herbivory varied by sites ($F_{3,24}$:1.71,P=0.0000037; Figure 2b) and time ($F_{1,24}$:1.73, P=0.0087; Figure 2b) . The interaction was not significant ($F_{3,24}$:0.94, P=0.44; Figure 2b). Mammal grazing was simliar among all sites except the invaded site, which had lower incidence of mammalian herbivory. Mammalian herbivory increased over time, but not in the invaded sites.

Total herbivory by insects was significanton sites ($F_{3,24}$:8.22, P=0.00061; Figure 2c). Time wasn't significant ($F_{1,24}$:0.44, P=0.51; Figure 2c) or neither the interaction($F_{3,24}$:1.07, P=0.38; Figure 2c) on total herbivory by insects. or Total herbivory by insect was greater in invaded sites and at sites with experimental removals of *L. dalmatica* than native site and sites with introduced native plants..

Species richness and abundance and functional groups

Sweep-nets

There was no significance difference in species abundance among sites ($F_{3,12}$ = 0.85, P=0.49; Figure 3a) and the in teraction of site and time ($F_{3,12}$:1.27, P = 0.33; Figure 3a) but there was a significant decrease in abundance over time ($F_{1,12}$ =8.10, P = 0.015; Figure 3a.. Species richness was not significantly different on sites ($F_{3,12}$ = 0.32, P = 0.81; Figure 4a) time ($F_{1,12}$:3.95, P =0.070; Figure 3a)or the interaction ($F_{3,12}$:1.04, p=0.41; Figure 3a). When evaluating different functional groups we found that there was no difference among sites for non-spider predators, scavengers and pollinators (Table 1) but there was a significance difference in spider and herbivore abundance over time, where spiders increased between sampling weeks and herbivores decreased (Table 1; Figure 5a and Figure 7a).

Pitfalls

Species abundance of invertebrates collected from pitfall traps did not vary significantly among sites ($F_{3,12}$:2.44, P =0.11; Figure 3b) time($F_{1,12}$:3.07, p=0.10; Figure 3b), or interacion($F_{3,12}$:0.32, p=0.80; Figure 3b). Similarly, species richness did not differ among sites ($F_{3,12}$:1.96, P =0.17; Figure 4b) time ($F_{1,12}$:0.093, P =0.77; Figure 4b) and their interaction($F_{3,12}$:0.27, P =0.84; Figure 4b). There was no significant difference on site, time or interaction on spiders, herbivores and pollinators (Table 1) There was a significant difference on predator and scavengers over time were predators decreased over time and scavengers increased over time (Table 1; Figure 6b and Figure 8b)

Discussion

Organism invasion is a situation often ignored and actions are made after a irreparable damage is done. Plant invasion is not the exception. Seeing the behavior of the shifts that herbivores and predators can do by plant invasion can help us understand more why invasion is successful and how can it affect an environment and how they can outcompete native plants. As an exotic plant becomes more abundant in an environment without natural enemies, native plants become limited and therefore limited food source for mammals and other native herbivores.

Herbivory

Invasive species can affect the environment in numerous ways. We expected to see more herbivory in native sites than invaded sites. However, our support of this hypothesis was mixed. Mammals preferred to graze more in native sites than in invasive sites, while insects preferred to feed in invasive sites. Differences in preferences by mammals and insects were masked when examining herbivory by all herbivores combined. Bison (Bison bison) prefer to eat grasses and this could be a reason why they preferred native sites where grasses where more abundant than in invasive sites. Insect herbivory was greater on native sites and a study made with native herbivores showed that generally they preferred exotic plants than native ones supporting our finding (Parker and Hay 2005).After one week of this experiments done, the sweep nets and pitfalls where preformed again. We found that total herbivory was not different among all sites but mammal herbivory was different in all sites. We found that native sites and sites with the introduction of *E. bellidiastrum* behaved equally with more herbivory by mammals supporting again the idea that mammals prefer to herbivorize on native sites or with native flora and further more on time the mammal herbivory increased, but this was because after one week the project began, bison where introduced in the sites. Sites invaded and where experimental removals of *L. dalmatica* behaved the same with more herbivory by mammals, perhaps the clipping of $0.625m^2$ wasn't enough to see a change of more herbivory by mammals and behaved more like a invasive site. Overall, generalist herbivores available in an environment like better to feed on exotic plants (Schaffner et. al 2011).

Invertebrate Responses

Our swee pnet data show that species abundance didn't vary among sites, but decreased significantly over time across all sites. . When evaluating functional groups, spiders increased over time in all four sites but herbivores decreased. Herbivores may have decreased because of the increased temperatures and plant senescence, meaning less food available for insect herbivores. Some herbivores are more sensitive to chemical changes in their secondary host plant, caused by environmental factors (Veteli et. al 2003), which may also explain the decline of some herbivores.

Pitfall trap data also showed no difference in abundance or richness of invertebrates among sites or over time We found that predators decreased over time and scavangers increased over time. As the season got drier and all plants were drying because of the lack of moisture the population of scavengers may have been greater by the accumulation of dead organic matter which they used as their food source.

Overall, even though there wasn't a difference in total herbivory rates, we can say that mammals prefer native sites over invasive and by the contrary insects prefer invasive. Species richness, abundance and the different functional groups wasn't affected by the invasion of *Linaria dalmatica* but temperature needs to be included in further research where they can see effects on temperatures, exotic plants and insects to see how it behaves on invaded areas versus native ones.

Acknowledgements

Thanks to my mentor Angela Laws for her support and guidance through this project. Thanks also to Diana Saintgnon who helped me do my field setup, collection and spiders and insect identification. Special gratitude to the Jose Enrique Fernandez who provided the funding for this program. Thanks to Nick Anderson and Jenny Lesko for insect identification. Last but not least, thanks to Gary Belovsky who accept me into this program and let me be part of it.

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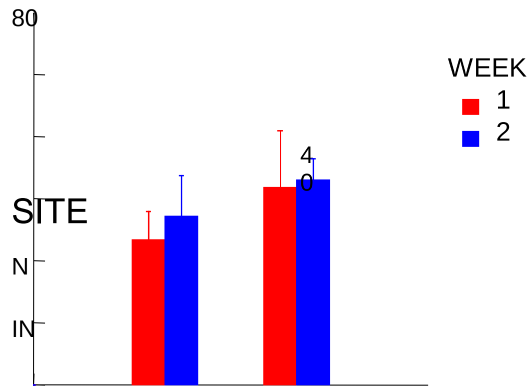
Apendix

Table 1

Sweep-nets Pitfalls

Group	**F-ratio**	**df**	**P-value**	**Group**	**F-ratio**	**df**	**P-value**
Spiders				*Spiders*			
Site	0.04	3,12	0.99	Site	0.54	3,12	0.66
Time	9.17	1,12	0.010	Time	4.29	1,12	0.060
Interaction	0.92	3,12	0.46	Interaction	0.63	3,12	0.61
Predators				*Predators*			
Site	0.81	3,12	0.51	Site	1.25	3,12	0.34
Time	3.20	1,12	0.099	Time	4.97	1,12	0.046
Interaction	0.81	3,12	0.51	Interaction	0.22	3,12	0.88
Herbivores				*Herbivores*			
Site	0.26	3,12	0.85	Site	1.46	3,12	0.27
Time	9.59	1,12	0.0092	Time	2.16	1,12	0.17
Interaction	1.01	3,12	0.42	Interaction	0.50	3,12	0.69
Scavengers				*Scavengers*			
Site	3.24	3,12	0.060	Site	2.00	3,12	0.17
Time	3.83	1,12	0.074	Time	4.20	1,12	0.000030
Interaction	1.73	3,12	0.21	Interaction	0.65	3,12	0.60
Pollinators				*Pollinators*			
Site	1.41	3,12	0.29	Site	0.50	3,12	0.69
Time	2.37	1,12	0.15	Time	0.50	1,12	0.49
Interaction	0.61	3,12	0.62	Interaction	0.046	3,12	0.71

a)



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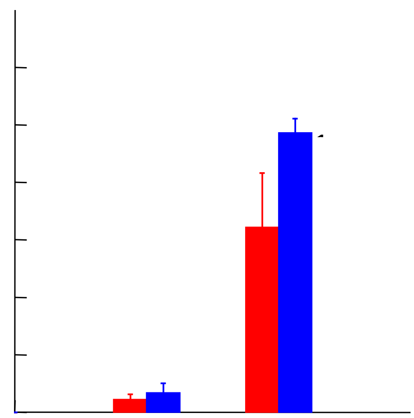

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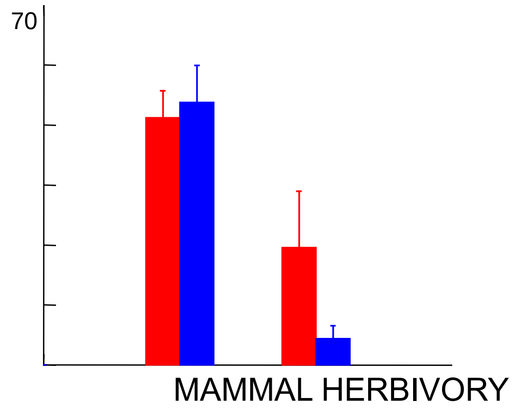
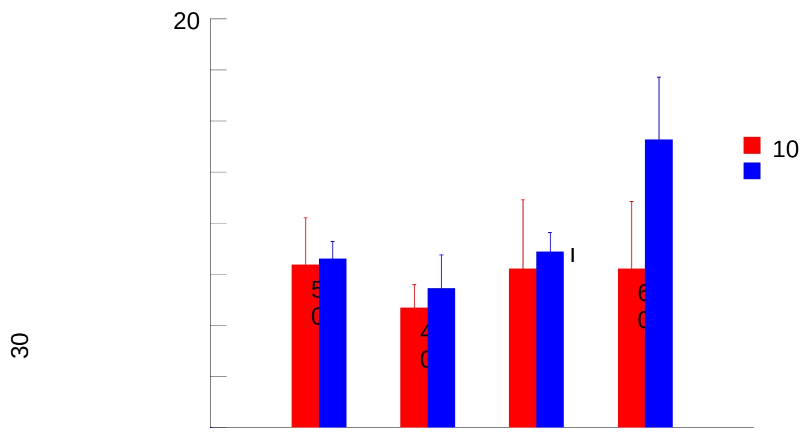


Figure 1. (a) Total herbivory between invaded versus native sites. (b) Mammal herbivory rate in invaded versus native sites. (c) Insect herbivory between invasive versus native areas.

a)



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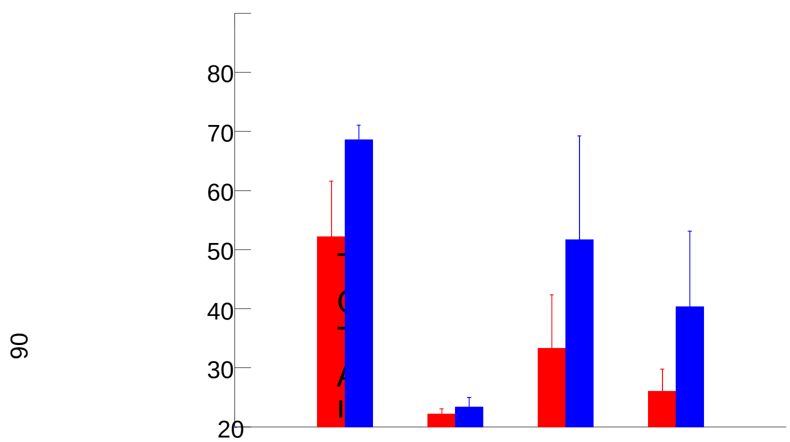

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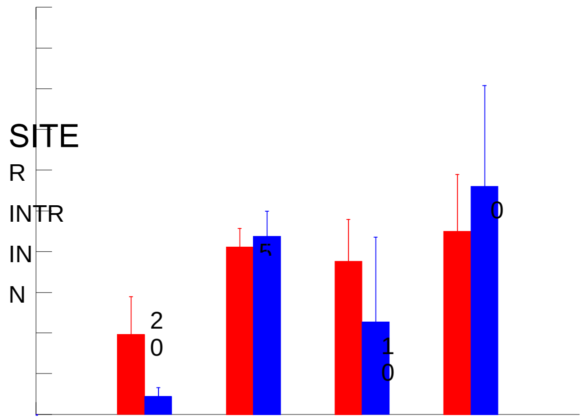
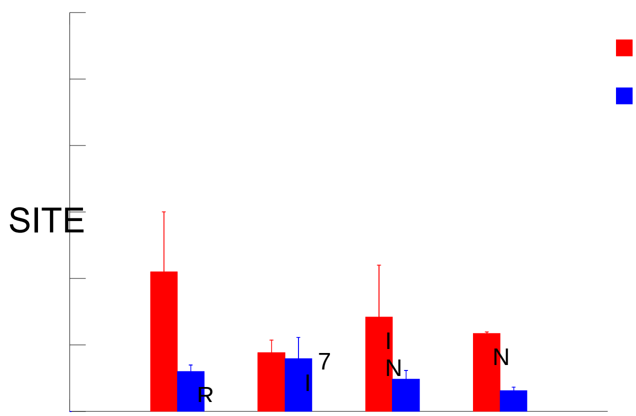


Figure 2. (a) Total herbivory among all sites. (b) Mammal herbivory among all sites (c) Insect herbivory among all sites.

(a)



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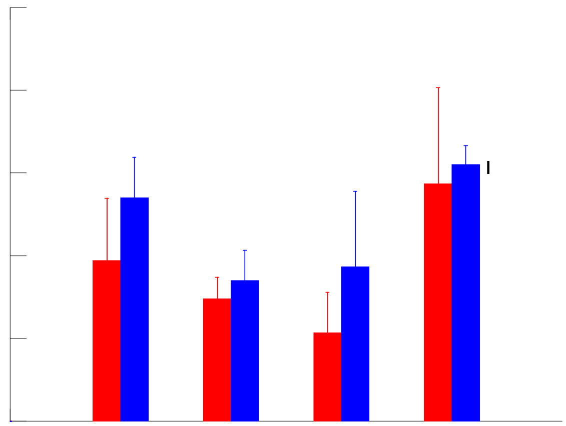
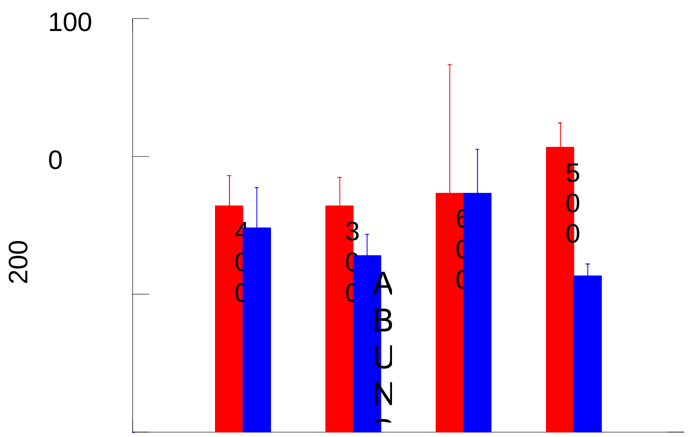
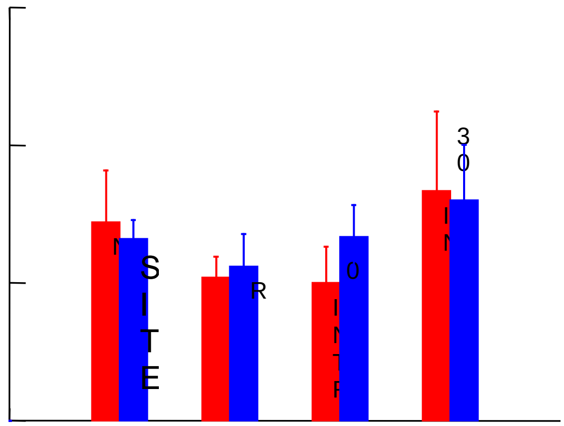


Figure 3. (a) Species abundance in sweep nets. (b) Species abundance on pitfall traps.

(a)

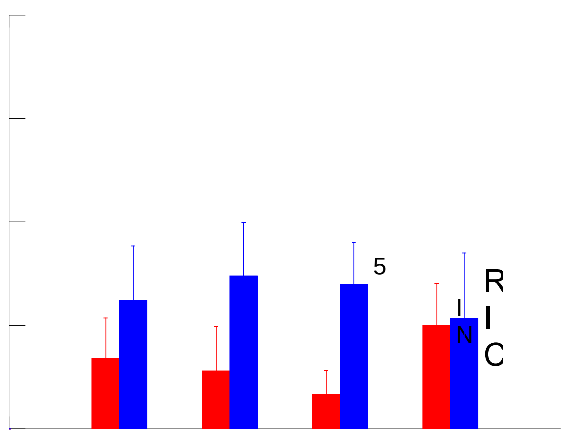




(b)

Figure 4. (a) Species richness on sweep nets. (b) Species richness on pitfall traps.

(a)



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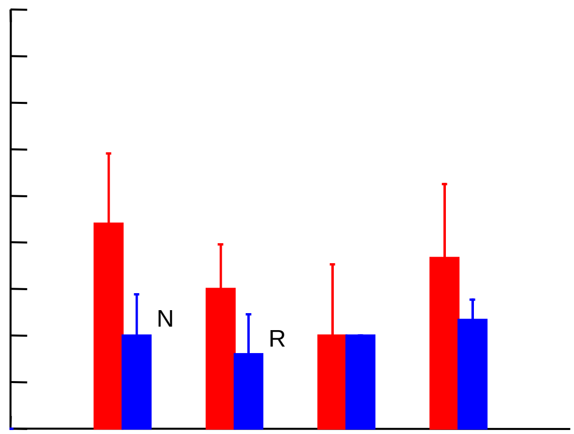
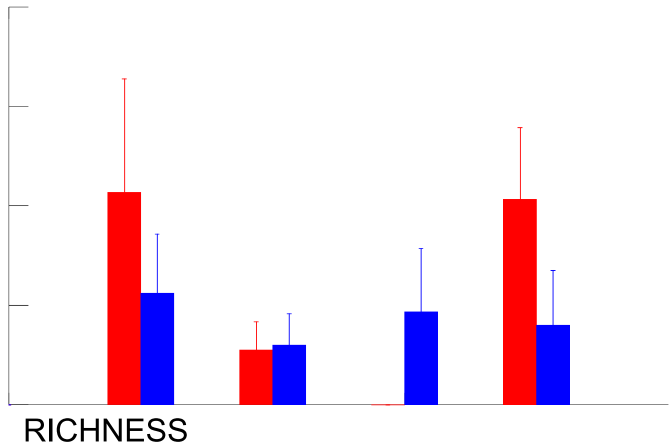


Figure 5. (a) Spiders among all site on sweep nets. (b) Spiders among all sites on pitfall traps.

(a)



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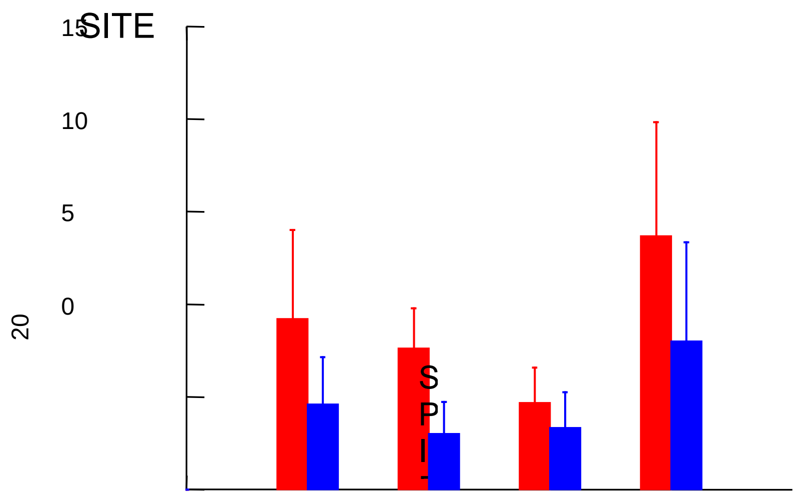
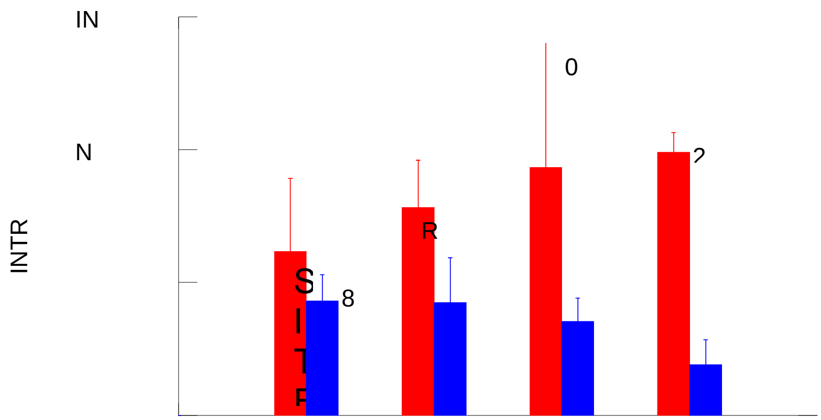


Figure 6. (a) Predators among all sites on sweep nets. (b) Predators among all sites on pitfall traps.

(a)



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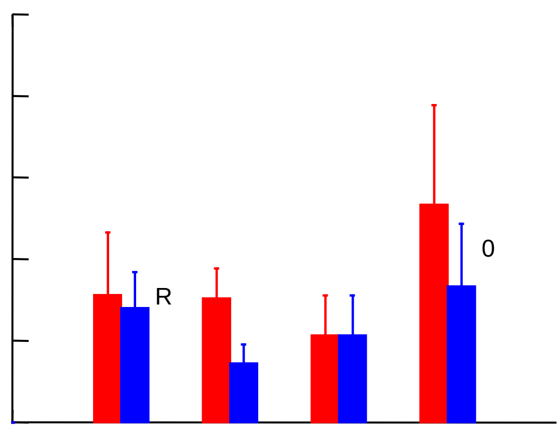
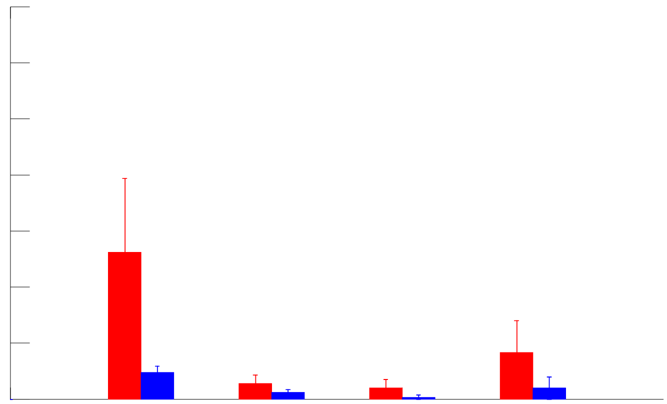


Figure 7. (a) Herbivores among all sites on sweep nets. (b) Herbivores among all sites on pitfall traps.

(a)



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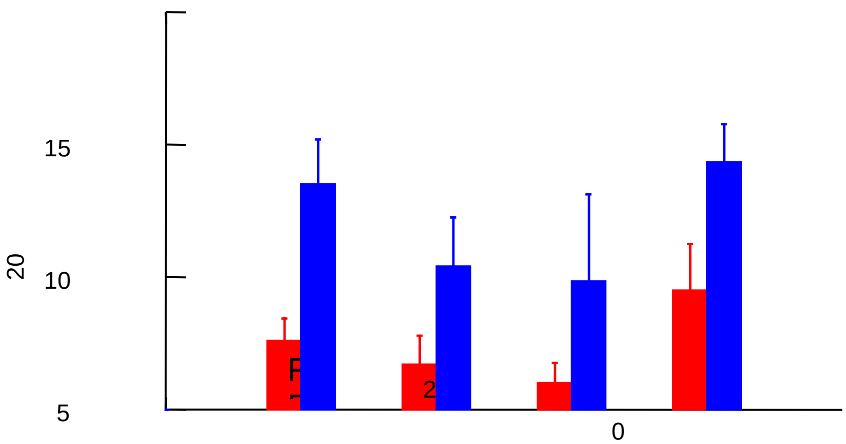
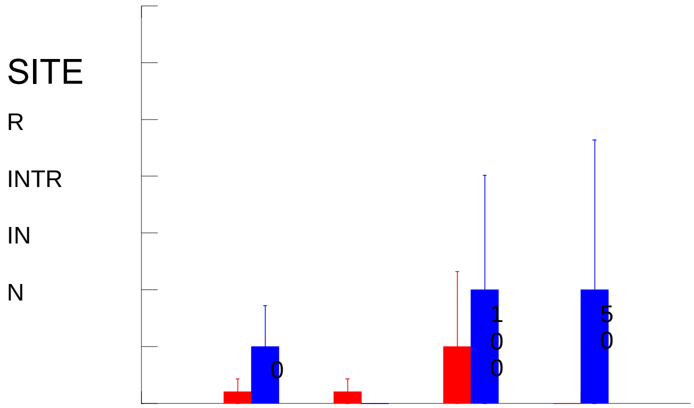


Figure 8. (a) scavengers among all sites on sweep nets. (b) Scavengers amons all sites on pitfall traps.

(a)



(b)

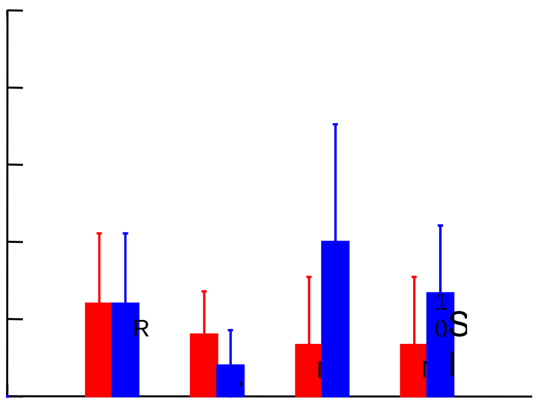


Figure 9. (a) Pollinators among all sites on sweep nets. (b) Pollinators among all sites on pitfall traps.