

## HOST-PLANT GENOTYPIC DIVERSITY MEDIATES THE DISTRIBUTION OF AN ECOSYSTEM ENGINEER

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**Abstract.** Ecosystem engineers affect ecological communities by physically modifying the environment. Understanding the factors determining the distribution of engineers offers a powerful predictive tool for community ecology. In this study, we examine whether the goldenrod bunch gall midge (*Rhopalomyia solidaginis*) functions as an ecosystem engineer in an old-field ecosystem by altering the composition of arthropod species associated with a dominant host plant, *Solidago altissima*. We also examine the suite of factors that could affect the distribution and abundance of this ecosystem engineer. The presence of bunch galls increased species richness and altered the structure of associated arthropod communities. The best predictors of gall abundance were host-plant genotype and plot-level genotypic diversity. We found positive, nonadditive effects of genotypic diversity on gall abundance. Our results indicate that incorporating a genetic component in studies of ecosystem engineers can help predict their distribution and abundance, and ultimately their effects on biodiversity.

**Key words:** community genetics; ecosystem engineer; genotypic diversity; goldenrod bunch gall midge; herbivory; host plant; plant–insect interactions; *Rhopalomyia solidaginis*; *Solidago altissima*.

### INTRODUCTION

Ecosystem engineers influence the distribution and abundance of other members in a community by providing shelter from the physical environment, protection from enemies, or increased availability of food resources (Jones et al. 1994). For example, dam-building beavers can dramatically alter the structure of stream and pond communities, influencing species diversity at multiple spatial scales (Wright et al. 2003). However, less conspicuous species can also act as ecosystem engineers (Cappuccino 1993, Martinsen et al. 2000, Lill and Marquis 2003). Shelter-building caterpillars modify the structure of leaves on host plants, forming habitats that are often secondarily used by other arthropods. As a result, these less conspicuous ecosystem engineers can increase the diversity of arthropods on plants and alter community composition (Martinsen et al. 2000, Lill and Marquis 2003, Crutsinger and Sanders 2005). Even though ecosystem engineers may be ubiquitous across ecosystems, much remains to be learned about both the

ultimate consequences of ecosystem engineers in communities (how they affect biodiversity) and the proximate causes of ecosystem engineering (what factors predict the occurrence of engineers in communities; Jones et al. 1994).

In this study, we first examine whether the goldenrod bunch gall midge, *Rhopalomyia solidaginis*, functions as an ecosystem engineer by altering plant architecture (see Plate 1; Appendix A) and affecting the structure of arthropod communities associated with its host plant, *Solidago altissima* (tall goldenrod). Though the insect fauna of *Solidago* is well studied (Hartnett and Abrahamson 1979, Abrahamson and McCrea 1986, Root and Cappuccino 1992, Raman and Abrahamson 1995), no studies to our knowledge have examined whether bunch-galling midges function as ecosystem engineers through their effects on the arthropod communities associated with *Solidago*.

In the second part of the study, we ask whether host-plant genotype and host-plant genotypic diversity (the number of genotypes per patch) affect the density of galls. Genetically based traits of host plants can influence gall-making species and the structure of associated arthropod communities (Whitham et al. 2006). Within old-field fragments, local populations of *Solidago* can contain clones that exhibit considerable

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trait variation, particularly in resistance to herbivores (Maddox and Root 1987, McCrea and Abrahamson 1987). The number of *Solidago* genotypes in natural patches of a few to thousands of ramets can vary from one to >12 genotypes/m<sup>2</sup> (Maddox et al. 1989). When particular genotypes of *Solidago* vary in their susceptibility to attack by gallers (Cronin and Abrahamson 1999), variation among patches in the number of genotypes could influence the density of galls. Patches containing several genotypes are more likely to contain a gall-susceptible genotype of *Solidago* than patches containing only one or a few genotypes.

Here, we use a series of manipulative experiments and an observational study to address two questions: (1) Is *R. solidaginis* an ecosystem engineer that alters the structure of the arthropod community associated with *S. altissima*? (2) What is the effect of host-plant genotype identity and patch-level genotypic diversity on gall abundance?

#### MATERIALS AND METHODS

##### *Is R. solidaginis an ecosystem engineer that alters the structure of the arthropod community associated with S. altissima?*

We did this work at Freel's Bend at the Oak Ridge National Laboratory (ORNL) National Environmental Research Park (NERP) near Oak Ridge, Tennessee, USA (35°58' N, 84°17' W; Appendix A). In July of 2005, we identified 20 distinct *Solidago* patches that were each a minimum of 10 m apart. In each patch, we randomly selected two pairs of *Solidago* ramets. Each pair contained a galled ramet and its closest ungalled neighbor of similar size. We visually surveyed arthropods on both ramets. We then collected the gall in a plastic bag and an equal length of stem from the ungalled neighboring ramet. These were taken back to the laboratory on ice and dissected under a dissecting microscope to count and identify all of the secondary users (excluding the galling midge, *R. solidaginis*) occurring inside the bunch gall and arthropods on the portion of ungalled stem to morphospecies. We classified each species into a trophic group based on its feeding morphology, observations in the field, and previous studies. Here, we focus on only the responses of herbivores and predators. For each galled and ungalled stem, we tallied the total number of individuals and species occurring on the ramet (visual scan and dissections of galls). We used two separate ANOVA models to determine whether patch (as a block) and host-plant status (galled or ungalled) affected arthropod richness and abundance (we excluded *R. solidaginis* as a component of the response variable in all analyses). We also used two separate ANOVA models to determine whether patch (as a block) and gall status (galled or ungalled) affected richness and abundance of herbivores and predators. To determine whether overall arthropod

community composition varied among galled and ungalled ramets, we used nonmetric multidimensional scaling (NMDS), a nonparametric analytical technique that is applied to a dissimilarity matrix calculated using the Bray-Curtis dissimilarity coefficient (Clarke 1993). Comparisons between the two communities on galled and ungalled plants were made using an analysis of similarity (ANOSIM) statistical test (Primer-E 2001). We did not use rarefaction because several of the samples contained no individuals.

We experimentally examined the effect of galling on the rest of the arthropod community. In June 2005, we bagged 12 ungalled ramets with bridal veil to decrease the probability that the ramet would be galled by *R. solidaginis*. The bags were left on the ramets until most gall initiation had terminated in late July. We grouped each of these bagged ramets with their closest galled ramet and an ungalled control ramet. Bags were removed and arthropods were allowed to colonize the ramets for one week. We then repeated the census techniques described previously. In this experiment, meadow spittlebugs (*Philaenus spumarius*) were present in high abundance on many of the ramets. We used two separate ANCOVA analyses to examine the effects of the treatment manipulation (bagged, galled, and control) and spittlebug density (as a covariate in the model) on total arthropod richness and abundance. Spittlebugs were a covariate in the model, and not included in the response, because they can affect the performance and distribution of other arthropods on individual ramets (Cronin and Abrahamson 1999). We followed these analyses with Tukey's multiple comparisons post hoc tests to separate means.

Galls could affect the associated community of arthropods in several ways. For example, the gall-making midge could act as an ecosystem engineer (in the true sense of the term) and create habitat for the rest of the community. Alternatively, the gall could alter host-plant chemistry, thereby affecting susceptibility to other herbivores. To test whether herbivores might preferentially forage on galled or ungalled leaf tissue, we performed a cafeteria experiment in 2005. We gave second-instar *Spodoptera exigua* larvae three choices of similarly sized leaves: a leaf from the gall of a plant, a leaf from a galled plant but not part of the gall, or a leaf from an ungalled plant. Ideally, we would use a species collected at the field site, but *S. exigua* larvae are commonly used in bioassays. Leaves were collected at the field site from 36 plants (18 galled and 18 ungalled) and were kept chilled on ice until the experiment commenced. In 18 petri dishes, we arranged these three leaf types so that they were equidistant from one *S. exigua* larva placed in the middle of the petri dish. After two days, we measured the percentage of the leaf area damaged by the larva. We used an ANOVA to examine whether caterpillar herbivory rates differed among

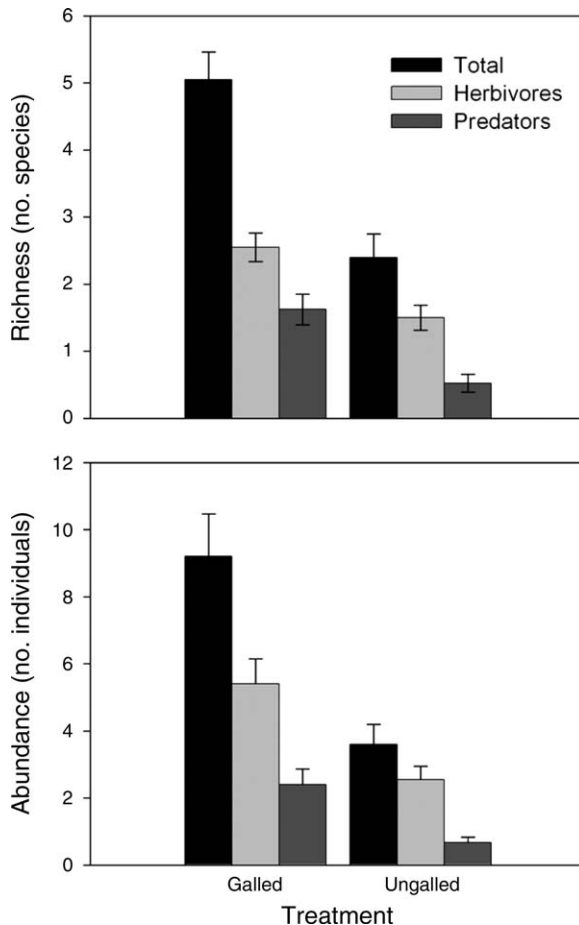


FIG. 1. Species richness and abundance (mean  $\pm$  SE) of total arthropods, herbivores, and predators, on paired galled and ungalled *Solidago altissima* ramets.

leaves from the galls, the stem of a galled plant, or the stem of an ungalled plant.

To examine whether more arthropods were associated with bigger galls as an indirect test of the hypothesis that galls simply provide habitat for arthropods, we examined the richness–gall area and abundance–gall area relationships using two separate linear regressions.

*What is the effect of host-plant genotype identity and patch-level genotypic diversity on gall abundance?*

To test how the genotype of *S. altissima* and the number of genotypes in a patch influence gall density, we constructed a common garden experiment consisting of 63 1-m<sup>2</sup> plots, each containing 12 ramets of *Solidago altissima*. The experimental treatments consisted of 21 genotypes grown in monoculture (two replicates of each) and diversity treatments containing 3, 6, or 12 different genotypes (seven replicates of each). In February 2005, we collected rhizomes from 21 ramets from local

patches, spatially separated by 50–100 m. We used amplified fragment length polymorphism (AFLP) techniques to ensure each ramet was a distinct genotype (for more detailed AFLP methods and common garden propagation, see Crutsinger et al. [2006]). Ramets were grown from rhizome cuttings under the same light, nutrient, and watering regimes in the greenhouse until April and then transplanted into 1-m<sup>2</sup> plots spaced 1 m apart in a 25  $\times$  15 m grid. Diversity treatments were created by randomly drawing from the pool of 21 genotypes with the stipulation that no two replicates within each treatment could overlap identically in composition. Ramets were planted evenly spaced in a circular design within each plot to ensure equal chance of colonization of galling midges (Crutsinger et al. 2006, Johnson et al. 2006).

In September 2005, we counted the total number of galls in each plot. We examined gall abundances instead of the proportion of *Solidago* ramets that were galled because we started the experiment with the same number of ramets in each plot ( $N = 12$  ramets per plot). To test whether total gall abundance varied among the 21 genotypes, we used a one-way ANOVA, treating individual monoculture plots as replicates. We examined the effect of genotypic diversity (1, 3, 6, or 12 genotypes) on gall abundance using linear regression. Because we found a positive relationship between gall abundance and genotypic diversity (see *Results*), we subsequently tested whether the effect of genotypic diversity on bunch gall abundance resulted from additive or nonadditive effects (i.e., the sum effect of each genotype's susceptibility to galling in a mixture; Crutsinger et al. 2006, Johnson et al. 2006; Appendix B). We also tested the effects of soil nutrient availability and landscape-level factors on gall density and found no effects (Appendix C).

## RESULTS

*Is R. solidaginis an ecosystem engineer that alters the structure of the arthropod community associated with S. altissima?*

When comparing paired ramets, arthropod species richness was 110% greater ( $F_{1,38} = 34.86$ ,  $P < 0.001$ ) and abundance was 150% greater ( $F_{1,38} = 17.87$ ,  $P < 0.001$ ) on naturally galled than on ungalled ramets (Fig. 1; Appendix D lists the taxa collected in this study). There was no patch effect on either richness or abundance ( $P > 0.08$  in both cases). Arthropod community composition differed significantly on galled and ungalled plants (ANOSIM;  $R = 0.32$ ,  $P = 0.01$ ) with only 27% overlap in overall species composition from a pool of  $\sim 50$  species (Fig. 2). The richness of herbivores was 70% greater ( $F_{1,38} = 17.33$ ,  $P < 0.001$ ), and abundance 110% greater ( $F_{1,38} = 18.53$ ,  $P < 0.001$ ) on galled than on ungalled ramets. Predator richness was 210% greater ( $F_{1,38} = 23.70$ ,  $P < 0.001$ ) and abundance 250% greater ( $F_{1,38} =$

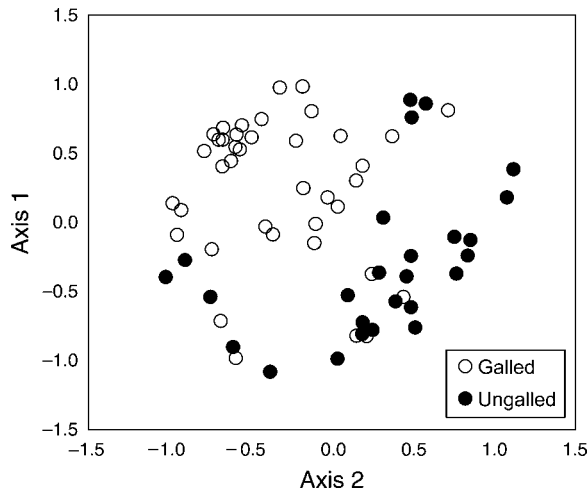


FIG. 2. Two-dimensional representation of arthropod communities occurring on galled and ungalled *Solidago altissima* ramets based on global, nonmetric multidimensional scaling (NMDS). Compositional dissimilarity originated from the presence or absence of 50 species of arthropods. In the figure, each symbol represents the community of arthropods associated with a particular plant. If communities on galled and ungalled stems were similar, the cloud of solid circles and the cloud of open circles would overlap more than they do.

16.85,  $P < 0.001$ ) on galled than on ungalled ramets (Fig. 1). We found no effect of patch identity on herbivore richness and abundance or predator richness and abundance ( $P > 0.12$  in all cases).

When we experimentally reduced galling rates, we found that galled ramets had significantly higher total species richness and greater abundance than did either bagged or control ramets ( $P < 0.05$ , Tukey's hsd). Bagged and control ramets did not differ in either richness or abundance ( $P > 0.05$ , Tukey's hsd; Fig. 3), and the abundance of spittlebugs did not affect either richness or abundance ( $P \geq 0.49$  in both cases).

We found no effect of leaf type (galled, ungalled, control) on herbivore damage by *S. exigua* caterpillars ( $F_{2,51} = 0.61$ ,  $P = 0.54$ ), indicating that galls were not attractive to herbivores because of changes in host-plant quality. Both arthropod species richness ( $r^2 = 0.21$ ,  $P < 0.01$ ) and abundance ( $r^2 = 0.15$ ,  $P = 0.013$ ) were positively and significantly related to gall area, suggesting that galls provide habitat for secondary users.

#### *What is the effect of host-plant genotype identity and patch-level genotypic diversity on gall abundance?*

Genotype identity of *S. altissima* affected gall abundance ( $F_{20,21} = 3.51$ ,  $P < 0.01$ ) with a 28-fold difference in gall abundance between the most susceptible (mean 29.5 gall/m<sup>2</sup>) and resistant genotypes (mean 1 gall/m<sup>2</sup>). Gall abundance was positively related to genotypic diversity ( $R^2 = 0.14$ ,  $P < 0.01$ ). There were 80% more galls in 12-

genotype diversity plots than in the one-genotype plots. There were also significantly more galls in the 12-genotype mixtures (three genotypes,  $P = 0.41$ ; six genotypes,  $P < 0.078$ ; 12 genotypes,  $P < 0.001$ ) than what is predicted from additive effects alone (Fig. 4).

#### DISCUSSION

Our results demonstrate that goldenrod bunch gall midges function as ecosystem engineers by providing habitat for a community of arthropod species in old-field ecosystems. The presence of galls increased arthropod diversity overall and consistently across herbivore and predator trophic levels. In addition, NMDS ordination revealed that galls alter the composition of arthropod communities associated with *S. altissima*. Experimental exclusion of galls confirmed that the presence of the gall, and not some other aspect of host-plant quality, shapes arthropod community structure. While other studies have shown that arthropod species function as ecosystem engineers (Cappuccino 1993, Martinsen et al. 2000, Lill and Marquis 2003), few studies have specifically linked the consequences of engineering with the factors that influence engineer distribution (Jones et al. 1994, Bailey et al. 2004). Our results indicate that of the biotic, abiotic, and spatial

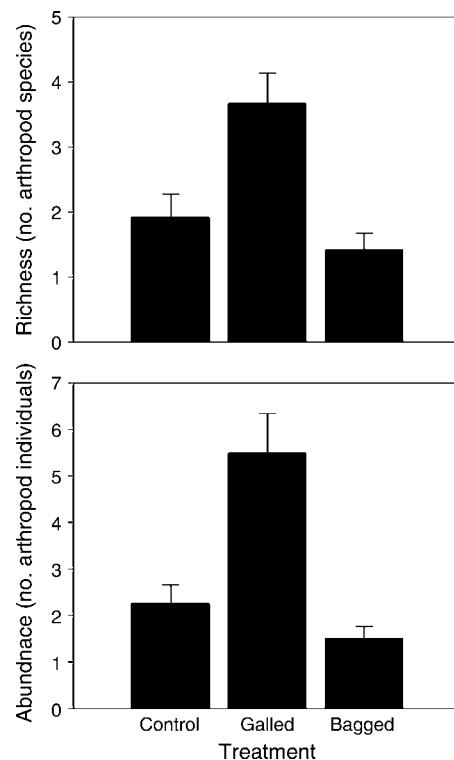


FIG. 3. Total arthropod species richness (mean  $\pm$  SE) and abundance (mean  $\pm$  SE) for galled, ungalled control, and bagged (gall excluded) *Solidago altissima* ramets.

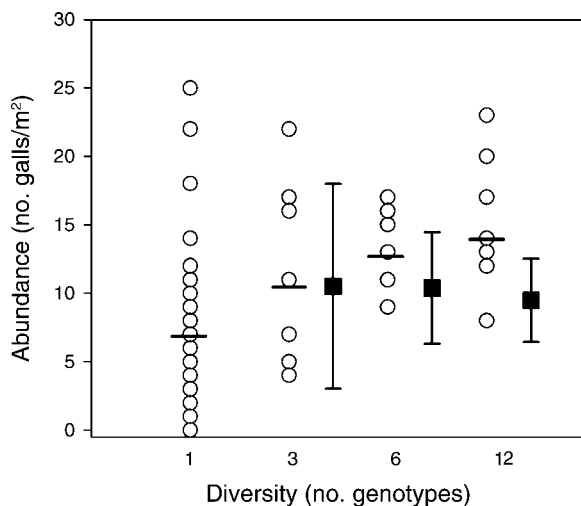


FIG. 4. The relationship between patch-level genotypic diversity and gall abundance. Open circles indicate plot-level observations, and the horizontal line indicates the treatment mean. The solid boxes show the number of galls predicted (mean and 95% confidence interval) by a simple additive model. If the confidence intervals overlap with the observed means, then additive effects of plant genotype susceptibility to galling can explain gall abundances in mixtures.

influences that we examined at our study site, only host-plant genotype and patch-level genotypic diversity influenced the abundance of *R. solidaginis* galls (Appendix D).

Arthropods may prefer engineered habitats for three reasons: (1) as refuges from predators, (2) as sites for preferential foraging, and (3) as protection from harsh environmental conditions. Leaf shelters can effectively reduce predation, providing a refuge for herbivorous arthropods (Damman 1987, Cappuccino 1993). It is unlikely that bunch galls in our system are used as a refuge from predators because we found more predators on galled ramets than on ungalled ramets. Galls might provide preferential foraging for herbivores if the galling midge induces a qualitative change in leaf structure or chemistry, as has been shown for leaf rollers (Sagers 1992). However, levels of herbivory on galled vs. ungalled leaves from our cafeteria experiment did not differ from one another. It seems most probable that the gall is used as a favorable microhabitat for both herbivores and predators. Direct manipulations of abiotic stress in the presence and absence of galls could help further resolve these putative mechanisms.

But is *R. solidaginis* an ecosystem engineer in the traditional sense of the definition (Jones et al. 1994)? Of course, beavers, gophers, and other classic ecosystem engineers can affect communities and ecosystems in dramatic fashion at multiple spatial scales. Invertebrate engineers, such as shelter-building caterpillars for example, increase diversity and structure arthropod

communities on cottonwood and oak trees (Martinsen et al. 2000, Lill and Marquis 2003). In their original papers Jones et al. (1994) posited that ecosystem engineers affect the rest of the community by purely physical modifications of the environment. It is well known that many galling species can affect host-plant chemistry (Hartley and Lawton 1992, Nyman and Julkunen-Tiitto 2000), but we suggest that our cafeteria experiment indicates that gall induction by *R. solidaginis* does not affect the community of secondary users by altering host-plant chemistry. Moreover, larger galls had more individuals and species than did smaller galls, suggesting that the secondary user community was responding to habitat availability rather than any chemical trait associated with galled plants.

Recent research has indicated that both host-plant genotype and genotypic diversity influence plant-herbivore interactions (Cronin and Abrahamson 1999, Johnson and Agrawal 2005, Wimp et al. 2005, Crutsinger et al. 2006, Johnson et al. 2006, Whitham et al. 2006), but few studies have shown that host-plant genotype can influence ecosystem engineers (Martinsen et al. 2000, Bailey et al. 2004). Martinsen et al. (2000) found that the abundance of engineering leaf rollers varies on backcross and  $F_1$  hybrid cottonwoods, indirectly altering arthropod community structure on trees of different genotypes. Similarly, we found that host-plant genotype influences the distribution of an engineer, which could, in turn, lead to landscape-level changes in arthropod community structure and diversity.

In addition, we found an 80% increase in the number of galls in 12-genotype plots compared to one-genotype plots. No other studies to our knowledge have shown that genotypic diversity can influence the distribution or abundance of an ecosystem engineer. At the highest genotypic diversity treatment of 12 genotypes, we found significant nonadditive increases in gall abundance with 54% more galls than what is predicted by simple additive effects. This nonadditive effect could be driven by associated susceptibility in genotypically diverse plots where the ramets of otherwise resistant genotypes are attacked by midges due to their close proximity to susceptible genotypes (Atsatt and O'Dowd 1976, White and Whitham 2000). Associated susceptibility may be common with herbivores and could lead to interesting interactions with arthropod communities occurring on resistant vs. susceptible genotypes. Future research that emphasizes the importance of intraspecific genotypic diversity within local populations for key members of communities, such as ecosystem engineers, would be informative (Wimp et al. 2005, Whitham et al. 2006).

In sum, galling by *R. solidaginis* significantly increases arthropod diversity and alters the structure of communities associated with *S. altissima*. We found strong extended consequences of host-plant genotype and



PLATE 1. Bunch gall on a *Solidago altissima* (tall goldenrod) plant induced by the midge, *Rhopalomyia solidaginis*. Photo credit: G. Crutsinger.

positive nonadditive effects of host-plant genotypic diversity on the abundance of galls. Taken together, our results indicate that to understand more fully the consequences of ecosystem engineers, it may be necessary to understand how genetic factors mediate the distribution of engineers and ultimately engineering effects on communities and ecosystems (Bailey et al. 2004).

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#### APPENDIX A

Natural history information and site description (*Ecological Archives* E088-126-A1).

#### APPENDIX B

Monte Carlo simulations to test for nonadditivity (*Ecological Archives* E088-126-A2).

#### APPENDIX C

The effects of soil nutrient availability and patch size and isolation on the abundance of bunch galls (*Ecological Archives* E088-126-A3).

#### APPENDIX D

Arthropod taxa encountered in this study (*Ecological Archives* E088-126-A4).