

Climate warming strengthens indirect interactions in an old-field food web

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Abstract. Climate change is expected to alter trophic interactions within food chains, but predicting the fate of particular species is difficult because the predictions hinge on knowing exactly how climate influences direct and indirect interactions. We used two complementary approaches to examine how climate change may alter trophic interactions within an old-field food web composed of herbaceous plants, grasshopper herbivores, and spider predators. We synthesized data spanning 15 years of experimentation during which interannual mean growing season temperature varied by 2°C and precipitation by 2.5 cm. We also manipulated temperature within mesocosms to test the affect of temperature on primary production and strength of direct and indirect trophic interactions. Both approaches produced similar results: plant production was not directly affected by temperature or precipitation, but the strength of top-down indirect effects on grasses and forbs increased by 30–40% per 1°C. Hence, the net effect of climate change was to strengthen top-down control of this terrestrial system.

Key words: climate change; grasshopper; indirect effects; insect herbivory; interaction strength; *Melanoplus femurrubrum*; old-field food web; *Pisaurina mira*; spider.

INTRODUCTION

Climate change stands to affect trophic interactions within ecological food chains (Petchev et al. 1999, Schmitz et al. 2003, Voigt et al. 2003, Vasseur and McCann 2005). Yet, making predictions about the particular fate of species in food chains is difficult because the predictions hinge on knowing exactly how direct and indirect effects will change as a consequence of changing climate (Schmitz et al. 2003, Emmerson et al. 2004, 2005, Vasseur and McCann 2005, Tylianakis et al. 2008). Species may respond to climate in tandem, with no net change in the indirect effect, or species may respond differently, leading to enhancement or weakening of the indirect effect (Harrington et al. 1999, McCarty 2001, Suttle et al. 2007, Tylianakis et al. 2008). Much uncertainty remains about the exact nature and strength of emergent effects because they are the net result of multiple species responding to multiple changes in their environment (Harrington et al. 1999, McCarty 2001, Suttle et al. 2007, Post and Pedersen 2008, Tylianakis et al. 2008).

There are two complementary ways to begin understanding the effects of a changing climate on direct and indirect trophic interactions. First, one can synthesize data collected from a temporal sequence of natural climate variation on the nature and strength of trophic interactions. Second, one can use an experimental approach that emulates conditions predicted by global

change models (Harrington et al. 1999). We present here an analysis of both kinds of data from a long-term research program in an old-field ecosystem composed of herbaceous plants, grasshopper herbivores (*Melanoplus femurrubrum*), and spider predators (*Pisaurina mira*). The data come from experiments conducted with these carnivore, herbivore, and plant species spanning a 15-year period, during which mean annual growing season temperature fluctuated by 2°C and precipitation doubled (2.5–5.0 cm) and from artificial warming of 2–4°C above ambient.

NATURAL HISTORY

This study was conducted within grassland ecosystems at the Yale-Myers Research Forest in northeastern Connecticut, USA near the town of Union. The summer (June–August) climate of this region is mild, with the daily maximum temperature averaging 22°C and monthly precipitation averaging 4 cm during the time frame of this study (1994–2008). Global change models predict this region will warm by 2–4°C and receive as much as 25% more precipitation by 2100 (U.S. Global Change Research Program 2003).

Long-term research has shown that the study system is largely driven by top-down control in which a spider acts as an indirect keystone predator whose effects are mediated by adaptive foraging of grasshopper herbivores (Schmitz 2004). In the absence of spiders, grasshoppers forage predominately on grasses and inflict considerable damage to them (Beckerman et al. 1997, Schmitz 1998). Predation by *P. mira* spiders is compensatory to natural grasshopper mortality. Hence grasshopper density was never reduced due to the presence of

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P. mira spiders (Schmitz 2004). Instead, spiders affect the system by altering grasshopper behavior. Grasshoppers respond to predation risk by reducing daily foraging activity (Rothley et al. 1997, Schmitz et al. 1997, Schmitz 2004), and shifting resource use to a competitively dominant forb, goldenrod (*Solidago rugosa*), which affords lower food quality but some refuge from predation risk (Beckerman et al. 1997). Consequently, the spider predator has an indirect positive effect on the abundance of grasses and an indirect negative effect on forbs.

This system is a good candidate for examining the effects of climate change on direct and indirect interactions within food chains because grasshoppers and spiders respond behaviorally to changes in climate. Total daily activity of grasshoppers is thermally constrained (Uvarov 1977, Belovsky and Slade 1986), and daily feeding time varies with temperature (Chase 1996, Pitt 1999, Rothley and Dutton 2006). Moreover, grasshoppers and spiders have different thermal tolerances, with grasshoppers being less prone than spiders to desiccation (Li and Jackson 1996, Joern et al. 2006). Grasshoppers can reduce predator encounters by becoming more active during the hottest parts of the day when spiders must reduce their activity to avoid thermal stress (Schmitz et al. 1997). Thus, warming may increase the proportion of the day in which spiders must remain inactive, decreasing the “window-of-opportunity” for spiders to prey upon grasshoppers (Joern et al. 2006). This suggests that warming may increase herbivory by decreasing top-down control and weaken the strength of the indirect effect of predators of plants. Moreover, high levels of precipitation can reduce grasshopper survival, reducing the effect of herbivory on plants (Ovadia and Schmitz 2004). Increased precipitation may also affect the system through bottom-up processes, such as increased soil moisture and nitrogen deposition, both of which can increase primary production and reduce top-down control in the system (Zavaleta et al. 2003, Galloway et al. 2004).

METHODS

Synthesis of past experiments

We synthesized published data from eight years of experiments examining top-predator effects in the same old-field system (Appendix A). All experiments followed the same standard protocols for mesocosm experiments evaluating top-down effects (Schmitz 2004), which involved systematically altering the number of trophic levels and measuring plant biomass in each trophic treatment at the end of the growing season. Experiments lasted for a single season and were conducted in different locations within the field each year, allowing us to treat each year's data as an independent sample. The focus of this analysis was on how the strength of top-down effects on plants (either directly through herbivory or indirectly through herbivore mediated predator effects) was related to interannual variability in temperature and precipita-

tion. We examined how climate affects trophic control of total plant biomass as well as biomass of grasses and forbs separately owing to potential climate effects on predator-induced diet shift by grasshoppers.

Heated field experiments

We conducted heating experiments during two years (1994 and 2008). These heating experiments perturbed the system beyond the mean summer temperature, as predicted by global change models for the region (U.S. Global Change Research Program 2003). We followed the same mesocosm experimental protocol to evaluate top-down effects as was described above (Schmitz 2004), using circular enclosures (1.0 m² basal area, 0.8 m tall; see Appendix A). Warming was simulated by securing commercially available plastic sheeting (Film-Gard, 4 mm; Covalence Plastics, Minneapolis, Minnesota, USA) to the outer infrastructure of each treatment cage, while leaving the top entirely open. This open top design did not inhibit rainwater from entering cages relative to unwrapped cages ($t_{1,4} = -0.73$, $P = 0.45$). The resulting “greenhouse effect” heated the cages an average of 3.9°C and 2.5°C above ambient temperatures in 1994 and 2008, respectively (B. T. Barton, *unpublished data*; A. P. Beckerman, *unpublished data*), which is within the range of temperature increase predicted for this region by 2100 (U.S. Global Change Research Program 2003). In both years, we randomly assigned heating treatments to cages containing one, two, and three trophic levels in the same field as the control cages used in the synthesis. Cages were stocked at natural field densities with grasshoppers (two trophic levels) or grasshoppers and spiders (three trophic levels) in early summer. After 100 days, we terminated the experiment and removed all above-ground biomass. We also recorded final grasshopper and spider densities and sorted vegetation into two functional groups: grasses and forbs (we only quantified total plant biomass in 1994). We weighed plants after drying at 60°C for 24 hours.

Data analysis

We measured biomass in one-level (N_1 , plants only), two-level (N_2 , plants and grasshoppers) and three-level food webs (N_3 , plants, grasshoppers, and spiders). We calculated the strength of the direct effect of grasshoppers on each group of plants as $\ln(N_2/N_1)$ and the strength of the indirect effect of spiders on each group of plants as $\ln(N_3/N_2)$. All experiments were conducted using a randomized block design. We therefore calculated the effect magnitude as the log ratio using companion two-level and three-level treatments within each block. For each year, we estimated the mean and variance in effect magnitude across all blocks. We did not quantify the strength of the direct effect of spiders on grasshoppers in the synthesis data because no net density effect was found in any of the experiments we reviewed. That is, grasshopper mortality from spider predation was compensatory to natural mortality and so

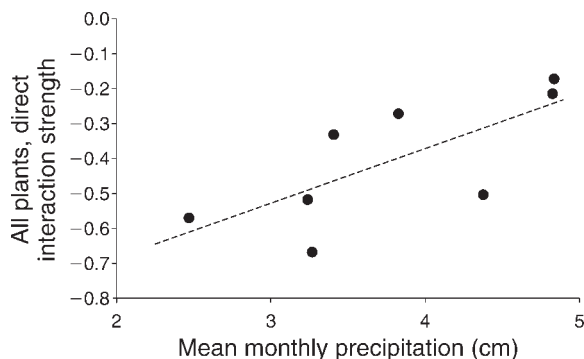


FIG. 1. The magnitude of the direct effect of herbivores on all plant biomass attenuated with increasing mean monthly rainfall in grassland ecosystems at the Yale-Myers Research Forest in northeastern Connecticut, USA. The strength of the direct effect of grasshoppers on plant biomass was calculated as $\ln(N_2/N_1)$, where N_1 is plant biomass in one-trophic-level treatments and N_2 is plant biomass in two-trophic-level treatments. See *Methods: Data analysis* for further details.

the net indirect effect of spiders on plants was always driven by grasshopper adaptive foraging shifts in response to predation risk.

The experiments measured plant response at the end of the summer growing season. As such, the plant response integrates the effects of seasonal temperature and precipitation over the summer. We therefore calculated the mean monthly temperature and precipitation for each summer (June–August) of each study year using the New England Climatological Data Annual Summary (Appendix A).

One-level plant-only treatments provided measures of aboveground net primary productivity (ANPP, $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) for that year (McNaughton et al. 1996). We related ANPP measures to the mean summer precipitation and temperature for the associated year to assess how much climate may have changed bottom-up control of this system.

Because experiments in different years were conducted with different sizes of mesocosms ($0.25\text{--}1\text{ m}^2$), we tested for a cage effect on interaction strengths. Finding no significant cage effect on plant biomass or interaction strengths (Appendix B), we scaled biomass estimates on a per m^2 basis to standardize biomass estimates among years.

We used the general linear models procedure in SYSTAT (Systat, Chicago, Illinois, USA) to test for effects of temperature, precipitation, and temperature \times precipitation interaction on total plant biomass, grass and forb biomass, and direct effect magnitude of herbivores on plants and indirect effect magnitude of predators on plants. We examined the effect of ANPP on interaction strength using linear regression. Finally we assessed whether climate could alter the degree of variability in effect magnitudes by regressing yearly temperature and precipitation on yearly variance in effect magnitude.

We used a two-way ANOVA to analyze the effect of changing the number of trophic levels and temperature

on grasshopper density and on plant biomass independently for the 1994 and 2008 warming experiments. When significant differences were detected, we used a Tukey test to determine if the strength of the indirect effect of predators on plants in our heated experiments differed from controls. We also evaluated how well our regression of the synthesized data could explain experimental outcomes. Using a *t* test, we compared interaction strengths calculated from the warming treatments with those expected for the same temperature based on the synthesis regression. We also examined the effect of heating on the variability of total plant biomass in one-, two-, and three-trophic-level treatments and on interaction strengths using *F* ratio tests.

RESULTS

Synthesis of experiments

All tests for significance of the regressions were based on $F_{1,7}$. ANPP was not affected by temperature (all plants, $P = 0.68$; grasses, $P = 0.79$; forbs, $P = 0.60$), precipitation (all plants, $P = 0.71$; grasses, $P = 0.67$; forbs, $P = 0.81$), or temperature \times precipitation interaction (all plants, $P = 0.90$; grasses, $P = 0.94$; forbs, $P = 0.88$). Temperature had no effect on the direct effect magnitude of grasshoppers on plant biomass (all plants, $P = 0.34$; grasses, $P = 0.06$; forbs, $P = 0.89$). Precipitation weakened the negative effect of grasshoppers on total plant biomass by 15% per 1cm increase in mean monthly precipitation (Fig. 1: $r^2 = 0.55$, $P = 0.04$), but had no effect on grasses ($P = 0.11$) or forbs ($P = 0.16$) independently. There was no temperature \times precipitation interaction on the direct effect of grasshoppers on plants (all plants, $P = 0.90$; grasses, $P = 0.94$; forbs, $P = 0.88$). Plant production did not influence the magnitude of the direct effect of grasshoppers on plant biomass (all plants, $P = 0.50$; grasses, $P = 0.99$; forbs, $P = 0.23$).

Spiders had no effect on total plant biomass (Fig. 2A: $P = 0.48$). However, spiders had a positive indirect effect on grasses, and the strength of this interaction increased more than 30% per 1°C increase in mean summer temperature (Fig. 2B: $r^2 = 0.73$, $P < 0.01$). Spiders had a negative indirect effect on forbs, and the strength of this interaction increased 40% per 1°C increase in mean summer temperature (Fig. 2C: $r^2 = 0.61$, $P = 0.02$). The indirect effect magnitude of spiders on plants was not affected by precipitation (all plants: $P = 0.80$; forbs: $P = 0.15$; grasses: $P = 0.06$) or by a temperature \times precipitation interaction (all plants, $P = 0.09$; grasses, $P = 0.051$; forbs, $P = 0.07$). The indirect interaction strengths on grasses and forbs were positively related ($r = 0.83$, $P < 0.01$). We found no affect of temperature or precipitation on the magnitude of variation in indirect effect magnitude of predators on grasses or on forbs (Fig. 2B, C: both $P > 0.35$).

Heated field experiments

We recovered all spiders from all mesocosms at the end of the experiments. We found no significant effect

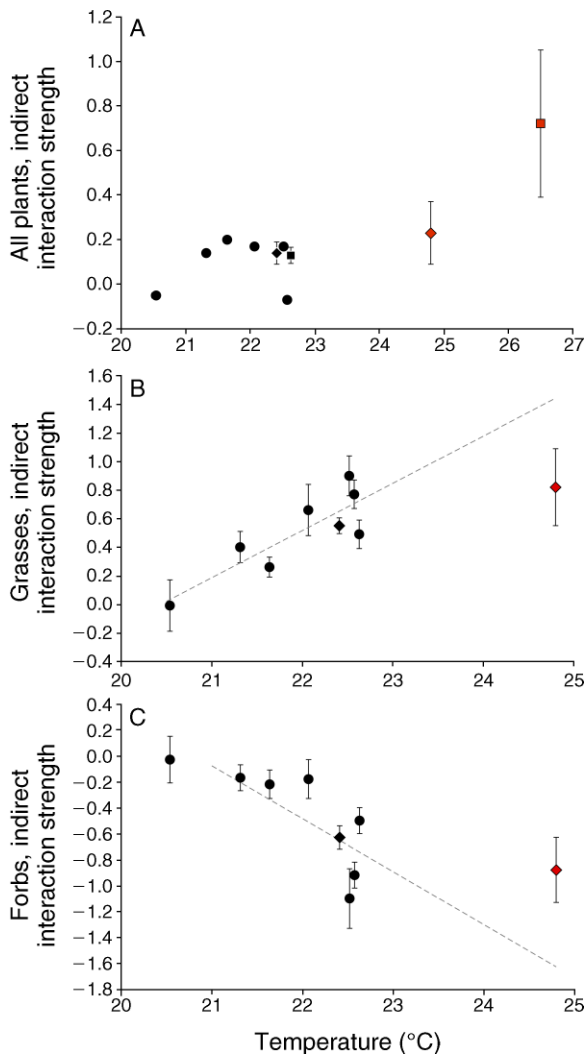


FIG. 2. (A) Temperature had no effect on the strength of the indirect effect of predators on total plant biomass in a synthesis of eight years of data (black symbols). However, experimentally warming mesocosms (red symbols) increased the indirect effect of predators on total plant biomass (squares = 1994, diamonds = 2008). Temperature increased the strength of the indirect effect of predators on (B) grass and (C) forbs in the synthesis data (black symbols). This regression analysis (broken lines) overestimated the magnitude of the indirect interaction strength in experimentally heated enclosures (red diamonds). Error bars represent \pm SE.

on final grasshopper density as a result of manipulating the number of trophic levels (ANOVA: 1994, $P = 0.35$, $df = 1, 7$; 2008, $P = 0.84$, $df = 1, 4$) or temperature (ANOVA: 1994, $P = 0.15$, $df = 1, 7$; 2008, $P = 0.09$, $df = 1, 4$). Trophic-level manipulations had a significant effect on total plant biomass in both years (1994, $F_{2,37} = 4.59$, $P = 0.02$; 2008, $F_{2,22} = 10.96$, $P < 0.01$), such that biomass was lower in two-level treatments than one- or three-level treatments (Tukey test, 1994, $P = 0.01$, $df = 1, 7$; 2008, $P = 0.01$, $df = 1, 4$). Temperature, however, did

not have an effect on total plant biomass in either year (ANOVA: 1994, $P = 0.10$; 2008, $P = 0.17$).

The heating treatment increased the strength of the indirect interaction compared to the control in 2008 for all plants (Fig. 3; $t_{1,4} = 3.33$, $P = 0.01$) and forbs ($t_{1,4} = 3.76$, $P < 0.01$) but not grasses ($P = 0.06$). Heating had no effect in 1994 (all plants, $P = 0.10$) owing to a high degree of variation within treatments in the 1994 heated conditions. The extreme warming treatment in 1994 ($>25^{\circ}\text{C}$) amplified variance in plant biomass in the three-trophic-level treatment ($F_{8,5} = 8.17$, $P = 0.03$), while variance was unaffected by warming for all other trophic-level combinations ($P > 0.05$). The magnitude of the indirect interaction in experimentally warmed mesocosms was accurately predicted by the linear regression of the synthesis data for grasses ($P = 0.08$; the observed interaction strength was not significantly different than the expected value predicted by regression), but overestimated the effect magnitude on forbs ($t_{1,4} = 3.0$, $P = 0.04$; the observed interaction strength differed significantly from the expected value).

DISCUSSION

Much research has been conducted to understand the effect of climate change on ecological communities, and much of this has aimed to predict how plants will

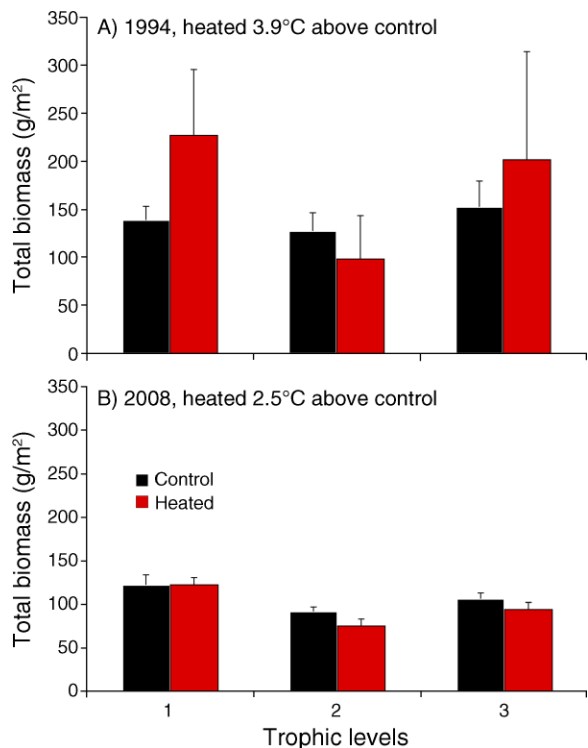


FIG. 3. Total plant biomass (mean \pm SE) from (A) 1994 ($n = 8$ replicate blocks) and (B) 2008 ($n = 5$) mesocosm experiments altering temperature across one (plants only), two (plants and grasshopper herbivores), and three (plants, grasshopper herbivores, and spider predators) trophic levels.

respond to changes in temperature and precipitation (Shaver et al. 2000, Zavaleta et al. 2003). This stems from a view that terrestrial systems are predominately controlled by bottom-up processes, in which characteristics of the plant community are the primary determinants of species abundances at higher trophic levels (Shaver et al. 2000). In this traditional view, we would expect temperature and precipitation to directly affect plants, which in turn would influence higher trophic levels. However, in a system characterized by strong top-down control, the effects of climate change on plants may be mediated by herbivory. Indeed, we present corroborating evidence from a synthesis of a long-term data set and a manipulative experiment that climate affected old-field plant communities indirectly by altering the strength of top-down control.

In a two-trophic-level system of interacting herbivores and plants, temperature did not alter the direct effect of grasshoppers on plants. Precipitation, however, reduced top-down control by weakening the negative effect of herbivores on total plant biomass at a rate of 15% per 1 cm increase of mean monthly rainfall. Because we found no effect of precipitation on ANPP, it appears that this reduced effect is a consequence of plants being released from herbivory rather than an increase in bottom-up effect. Indeed, the strength of the direct effect of herbivores on plants was not related to mean ANPP. The reduced effect of grasshoppers on plants is brought about by precipitation-induced grasshopper mortality, as grasshopper survival in this system is negatively associated with total precipitation (Ovadia and Schmitz 2004).

Our synthesis and field experiment demonstrated that top-down control on grasses and forbs strengthened with temperature in three-trophic-level food webs. The effect magnitude of spiders on grasses and forbs increased with temperature at a rate of approximately 30% and 40% per 1°C, respectively. This is opposite of what one might expect based on consideration of differences between grasshopper and spider thermal tolerances, where warming should decrease spider activity and, consequently, reduce the indirect effect of spiders on plants. Thus, we conclude that physiology alone does not sufficiently explain how climate alters interactions in this community.

The strengthening of the spider's effect on plants may be a consequence of how grasshoppers balance thermal and predator cues. Spiders indirectly affect plants by altering grasshopper diet composition (Rothley et al. 1997). Grasshoppers generally prefer to eat grasses, but increase their consumption of forbs in the presence of spider predators (Beckerman et al. 1997, Schmitz 2004). Consequently, spiders have an indirect positive effect on grasses and an indirect negative effect on forbs. While warming can directly reduce spider activity (Joern et al. 2006), it nevertheless seemed to enhance the ramifying effects of spiders in the community. This may be brought about because grasshoppers respond to the

presence of spiders by maintaining the diet shift toward forbs, without being affected by the predator's location or behavior (e.g., hunting in the canopy vs. inactive within the leaf litter; B. T. Barton, *unpublished data*). Thus, warming may have increased grasshopper feeding time (Chase 1996, Pitt 1999), without affecting diet composition thereby leading to heightened effects on both plant groups.

Our synthesis revealed that variation in indirect effect magnitude did not vary with temperature or precipitation. However, experimentation revealed that warming could cause a rise in variation in effect magnitude, but only for extreme warming (cf. 2008 vs. 1994: Fig. 2A). The difference between the two warming experiments is that the 2008 experiment elevated temperatures by 2.4°C whereas the 1994 experiment pushed the system almost 4°C warmer, which represents extreme warming for this region (U.S. Global Change Research Program 2003). Variation in effect magnitude for the 2008 warmed treatments was similar to that observed in the synthesis data (Fig. 2A). However, variation in the 1994 data was significantly larger. Because the variation seemed to increase abruptly beyond 25°C (Fig. 2A) we hypothesize that this represents a threshold where both the degree of change in effect magnitude and its associated variation rapidly increase once this temperature is surpassed.

Terrestrial communities are controlled by the interplay of bottom-up and top-down processes (Post et al. 1999, Schmitz 2003, Suttle et al. 2007). In systems characterized by strong bottom-up control, the effects of climate change are likely to be manifest directly at the plant level (Shaw et al. 2002, Weltzin et al. 2003, Zavaleta et al. 2003). However, in systems with strong top-down control, the increased sensitivity of higher trophic levels to climate change is a fundamental consideration when predicting how the system will respond in the future (Voigt et al. 2003, Post and Pedersen 2008). As shown here, climate can affect trophic interactions antagonistically: the strength of the direct effect decreased with precipitation, while the indirect effect increased with temperature. Thus, the net effect of climate change on ecological communities will be dependent on the relative strengths of bottom-up and top-down processes.

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APPENDIX A

Climate data and references for each climate year (*Ecological Archives* E090-164-A1).

APPENDIX B

Results from statistical analysis of the effect of cage size (*Ecological Archives* E090-164-A2).