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Biological control of yellow starthistle (*Centaurea solstitialis* L): prospective analysis of the impact of the rosette weevil (*Ceratapion basicorne* (Illiger))

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ABSTRACT

1. Yellow starthistle (*Centaurea solstitialis* L) (YST) is an invasive noxious weed that is native to the Mediterranean region with a geographic center of diversity in Turkey. It is widely established in Chile, Australia, and western North America. It arrived in California as a contaminant in alfalfa seed in 1859 and by 2002 had infested >7.7 million hectares in the USA.
2. Biological control of YST using capitula (seed head) feeding weevils and picture wing flies and a foliar rust pathogen has been ongoing in the western USA for more than three decades, but with limited success. Modeling and field research suggest that natural enemies that kill whole plants and or reduce the seed production of survivors would be the best candidates for successful biological control. A candidate species with some of these attributes is the stenophagous rosette weevil *Ceratapion basicorne* (Illiger).
3. In this paper, we add a model of the biology of the rosette weevil to the system model of YST and the capitula feeding natural enemies (Gutierrez et al. 2005), and use it to examine prospectively the biology of the weevil in the Palearctic region and its potential impact on the control of YST in the Western USA.
4. The results suggest that densities of mature YST plants in the western USA would be reduced in many areas 70-80 percent by the added action of *C. basicorne*.

INTRODUCTION

Pimentel et al. (2000) estimated total US annual costs due to invasive weeds in pastures is approximately $6.0 billion, with 83% of the costs due to recurring control costs rather than ongoing direct losses and damages. In contrast, biological control of invasive species is a proven tactic that should have high priority, but the question of how to assess the potential impact of prospective natural enemies for release across large areas with different climates and in the face of climate change remains vexing (e.g., Gutierrez et al. 2001; Gerard et al. 2013, Selvaraj et al. 2013). Yellow starthistle (*Centaurea solstitialis* L. (Asteraceae)) (i.e., YST) is one of the most important weeds in the Western USA (DiTomaso et al. 2006), and in this paper we assess prospectively the potential for its biological control.

YST is native to the Mediterranean region of southern Europe, Eurasia and North Africa (i.e. the Mediterranean Basin) with the geographic center of diversity thought to be in Turkey (Uygur et al. 2004). Eriksen et al. (2014) using nuclear sequence repeat markers, suggest that the center of diversity and the native range of YST is likely the eastern Mediterranean region in the vicinity of Turkey, that YST colonized other parts of Europe and Asia via a slow stepwise range expansion, with Spanish populations being the primary source of seed to invade South America, that North American populations of YST largely originated from South America, and that both North and South America had multiple contributions from secondary sources. YST was first recorded in the USA near San Francisco Bay in 1859 and by 1985 had infested over 3.24 million hectares in California (Maddox and Mayfield 1985), and it is now widespread in western North America. YST is toxic to horses, adversely affects native plants and wildlife, and heavy infestations affect the value of land for grazing and recreation (Pitcairn et al. 2006; DiTomaso et al. 2006). The full extent of the affected areas in the Western USA is not known, but it was estimated at >7.7 million hectares in 2002 with the highest concentrations occurring in California (Duncan 2001; Zouhar 2002).

Successful biological control of some weeds has occurred in North America (Huffaker and Kennett 1959; Hinz et al. 2014; Pitcairn et al. 2014), but biological control of YST has been elusive despite more than three decades of introducing and establishing capitula (i.e. seed head) feeding insects (e.g., the weevils *Bangasternus orientalis* (Capiomont), *Eustenopus villosus* (Boheman) and *Larinus curtus* Hochhut (Coleoptera: Curculionidae), and the picture winged flies *Chaetorellia australis* Hering and *Urophora sirunaseva* (Hering) (Diptera: Tephritidae))

(DiTomaso et al. 2006, Pitcairn et al. 2008, 2014) and a foliar rust pathogen (*Puccinia jaceae* var *solstitialis*) that appears to have little impact (O'Brien et al. 2010, Woods et al. 2010). The capitula fly *Chaetorellia succinea* (Costa) (Tephritidae) was accidentally introduced into southern Oregon in 1991 and is now widely established (Balciunas and Villegas 2007; Pitcairn et al. 2008). *L. curtus* and *C. australis* are not common in the field, and appear to contribute little to the control of YST. YST populations have not decreased greatly in many areas of California, Washington and Idaho (Piper 2001; Gutierrez et al. 2005; Pitcairn et al. 2006; Birdsall and Markin 2010).

Additional capitula feeding natural enemies occur throughout the Mediterranean Basin, but have not been introduced to North America (Sobhian and Zwölfer 1985; Rosenthal et al. 1994) (e.g., the weevil *Larinus filiformis* (Coleoptera: Curculionidae), an unidentified mordellid, and a gall-forming wasp *Isocolus scabiosae* (Giraud) (Hymenoptera: Cynipidae) (Gültekin et al. 2008, Uygur et al. 2012). In Turkey, the action of capitula feeding insects reduces seed production ~52% in attacked capitula, but only 5 to 55% of capitula are attacked (Uygur et al. 2012). In California, 49 to 89% of capitula are attacked (Pitcairn et al. 2005) with similar reductions in capitula seed production. However, despite lower capitula attack rates in Turkey mature YST plant densities are about 4% those in California. This suggests that other factors are limiting YST in Turkey (Uygur et al. 2012).

Field observations (Uygur et al. 2004) and modeling analysis (Gutierrez et al. 2005) suggest that natural enemies that kill whole plants before seed maturation and/or reduce the ability of surviving plants to compensate for feeding damage with reduced seed production are required for successful control (see below). The weevil (*Ceratapion basicorne* (Illiger) (Coleoptera; Brentidae)) attacks the rosette stage of YST throughout most of its range in the Mediterranean Basin (Alonso-Zarazaga 1990, Antonini et al. 2009), it has some of requisite attributes, infestation levels range from 25–100% (Uygur et al. 2005; Smith et al. 2006), and it is highly host specific (Smith et al. 2006, Smith 2007, 2012, Rector et al. 2010, Cristofaro et al. 2013). A release permit application for *C. basicorne* for North America was submitted to USDA-APHIS on 26 January 2006 (Smith 2006), but approval has not been granted because of concerns about possible risk to safflower crops (*Carthamus tinctorius*) and the ornamental cornflower (*Centaurea cyanus*) that are of Palearctic origin (Hinz et al. 2014, L. Smith pers. comm.).

In this paper, we first review the biology of YST and its interaction with the rosette weevil and then develop a model for *C. basicorne* and add it to the YST system model (Fig. 1a). The goal of our study is to assess prospectively the relative contribution of *C. basicorne* for added control of YST in the western USA. Readers are referred to Gutierrez et al. (2005) for details concerning the models of the capitula feeding insects in this study.

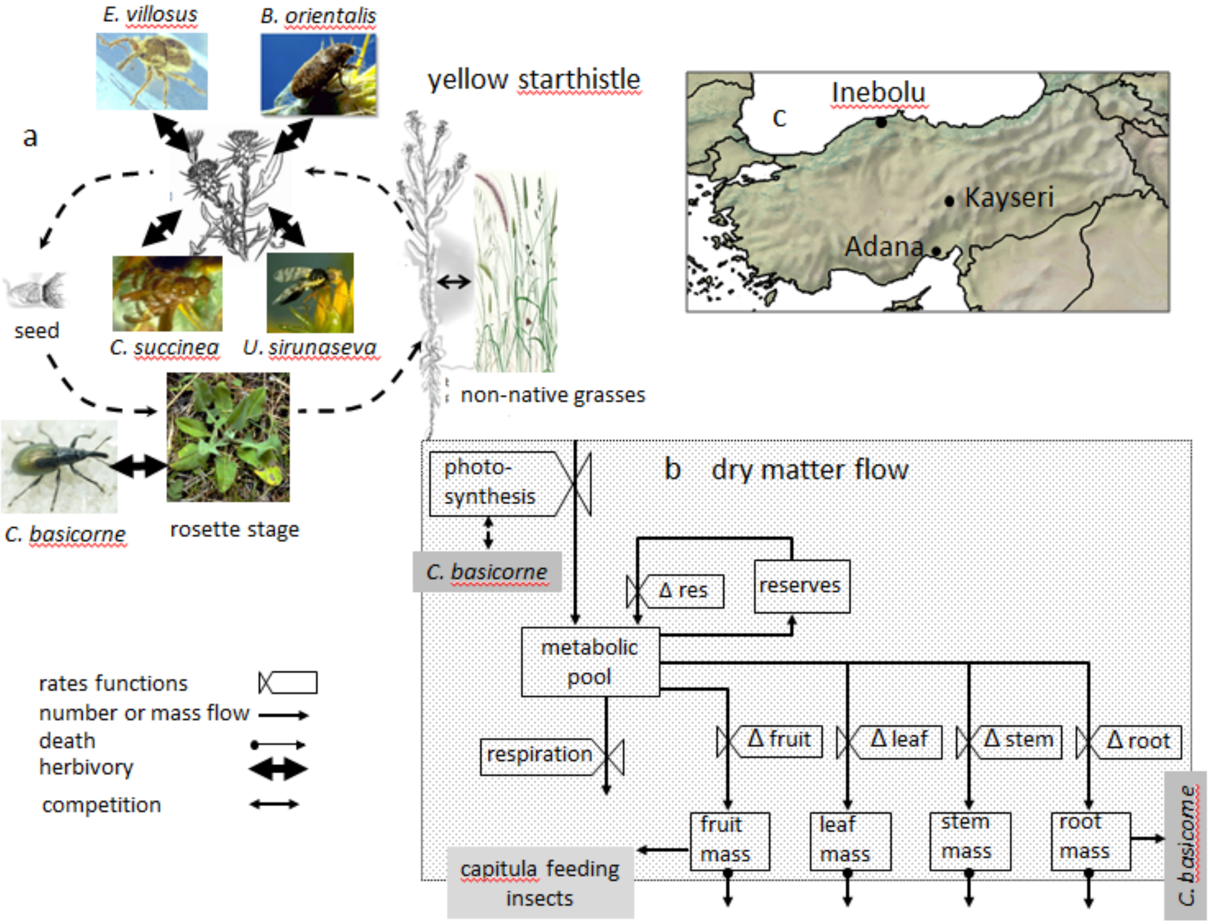

Figure 1. The interaction of yellow starthistle (YST) and the five herbivorous natural enemies: (a) the life cycle of YST and the points of attack by the natural enemies, (b) the dry matter flow rates in YST and the points of impact of the natural enemies, and (c) an inset of a map of Turkey showing the north to south locations of Inebolu, Kayseri and Adana respectively (see text). In sub figure 1a, the outer dashed curved arrows indicate the annual cycle of YST, the open thick double ended arrows indicate herbivore-host plant interactions and the thin solid double arrow competition between YST and grasses. Interactions between the capitula feeding herbivores are direct competitive interactions (see Gutierrez et al. 2005), while the effect of the rosette weevil on them is indirect via reductions in photosynthesis and plant growth. All photos of the organisms in composite figure 1a are from free access sources on the web.

Biology of YST

The developmental stages of yellow starthistle are the cotyledon, seedling, rosette, bolting, budding and later phases of capitula (seed head) production and development (i.e. flowering stage). YST is a winter annual that usually germinates in the fall with the start of the rainy season, and grows to the rosette stage during the winter, bolts in spring, and flowers continuously until the plants senesce from lack of water or are killed by freezing temperatures (Gutierrez et al. 2005; DiTomaso et al. 2006). Rosettes can survive the winter under snow, and additional seeds may germinate during spring rains. Growth of YST is assumed to occur at temperatures >8°C (Gutierrez et al. 2005).

YST does not use phytotoxic root exudates (allelopathy) in competition with grasses and other plants (Qin et al. 2007). Its invasive success in the Western USA may be enhanced by local morphological and phenological adaptations as an invasive weed in newly invaded areas (Eriksen et al. 2012), and increased resource use in the vacant niche created when native perennial grasses began to be replaced by exotic annual grasses starting in the late 1800s (Dlugosch *et al*. 2015). Using glasshouse studies and climatic niche modelling based on principal components analysis, Dlugosch *et al*. (2015) found YST in invaded areas has evolved a higher-fitness life history at the expense of increased dependence on water resulting in larger plants and higher reproduction. Spencer et al. (2011) fond that intraspecific competition among YST plants exerts a greater influence on mean plant weight than does interspecific competition from exotic annual grasses because: (1) yellow starthistle depletes soil moisture to less than 5% to a depth of 270 cm compared to say wild oats which reduces soil moisture only to a depth of approximately 150 cm, and (2) there is temporal separation of their phenology. Because soil moisture can be a limiting factor for YST in arid areas, a biophysical model (Ritchie 1972) is used to compute the soil water balance of rainfall and runoff above the holding capacity, and evapo-transpiration from the plant and the soil surface (see Gutierrez et al. 2005).

High densities of YST are observed in overgrazed disturbed areas in the western USA, and depending on plant density, soil moisture and competition, seed production may be as high as 12,000 seed m^{-2} (DiTomaso et al. 2006). The relationship of seed production to plant density suggests a plateau at 5,000 to 8,000 seed m^{-2} (see Gutierrez et al. 2005; Fig. 1b) which is 6-8 fold lower than the 500 million seeds per hectare posited by DiTomaso and Gerlach (2000). On average, healthy capitula produces 27-32 seed (M.J. Pitcairn, unpublished data). Buried seeds can persist for up to ten years under some field conditions, but if not replenished, seed viability near the soil surface decreases rapidly because of germination and destruction by arthropods and microbes (Joley et al. 2003). Dense populations of seedlings occur in many areas in the western USA, but often only a small proportion survive to reach reproductive maturity (Shelley and Larson 1994; Pitcairn et al. 1995, 2000).

Biology of the rosette weevil

Ceratapion basicorne females emerge from hibernation in early spring and feed and oviposit on the leaves of rosette stage plants, and upon hatching, the larvae burrow into the crown and upper root where they develop to the adult stage (Smith and Drew 2006). New adults emerge in late spring at the time the plants are bolting, and remain in reproductive quiescence until the next spring. Adults aestivate/hibernate in sheltered sites such as curled foliage or under tree bark (Hayat et al. 2002). In laboratory studies at 19°C, the developmental period from egg to adult emergence was 77 days, the mean oviposition period of adult females was 20.6 days (range 3-42), average lifetime fecundity was 34.5 eggs with a range of 1-87, and all females were alive after 45 days (Smith and Drew 2006). The sex ratio of adults reared from field collected immature stages in Turkey was approximately 1:1.

All field studies on the rosette weevil have been from the Palearctic region. In Italy, *C. basicorne* was found to infest an average of 40% of YST plants (range 12.2-55%) with an average of 1.97±0.95 larvae per plant with a range of 1-5 (Clement et al. 1989). In central and southern Turkey, Uygur (2004) reported a mean area covered by YST of 22.6% (range 3-30%) with a *C. basicorne* infestation rate of 18.4%. Rosenthal et al. (1994) reported 50–97% infestation; Smith et al (2006) found 48-100% infestation in field garden studies, while Balciunas and Korotyaev (2007) found an average 58% infestation across 20 sites. Uygur et al. (2005) reported that at least 50% of the root crown area was damaged in 63% of YST plants in southern Turkey. The number of larvae per plant was positively correlated to root diameter with aggregation occurring both among plants and within plants (Balciunas and Korotyaev 2007).

Rosette weevil infestation may have a large impact on plant size, reproduction and survival (Smith 2006), especially where plants compete for water, nutrients and light. This is the scenario observed in California for Klamath weed (*Hypericum perforatum*) which is attacked and controlled by the root feeding beetle (*Chrysolina quadrigemina*) (Huffaker and Kennett 1959).

Furthermore, as has been observed for *Larinus minutus* on diffuse knapweed (Piper 2004), rosette weevil adult feeding on rosette leaves in the spring may cause significant damage. In a field study in Turkey, up to seven *C. basicorne* larvae were found in some YST roots, reducing viable seed production by 15% (Uygur et al. 2005). Greenhouse experiments show that infestation of 4.2 ± 3.0 larvae per plant caused 23% reduction in the size of well-watered, fertilized potted plants (Smith 2006).

MATERIALS AND METHODS

YST system model

The use of weather driven physiologically-based models of crop plants have a long history in agriculture (Gutierrez et al. 1975; de Wit and Goudriaan 1978), and with demography added they become suitable for the analysis of tritrophic systems such as YST (Gutierrez and Baumgärtner 1984). These models are deterministic and fall under the ambit of physiologically-based demographic models (PBDM). Our PBDMs of the YST system (Fig. 1) are based on the distributed maturation time demographic models of Manetsch (1976) and Vansickle (1977) wherein developmental times of cohort members have a mean developmental times and variance (see appendix). The underpinning mathematics of the PBDM approach is reviewed in the appendix.

As applied to YST, the PBDMs enable capture of the interactions of plant-herbivore-natural enemy interactions as driven by weather, and enable the separation of the effects of weather from the impact of natural enemies. When well parameterized, the predictions of PBDMs can be compared to field data (e.g., Gutierrez and Ponti 2013). The PBDM for YST reported in Gutierrez et al. (2005) integrates the bottom up effects of weather and intra- and inter-specific competition for light and water with annual grasses, and the effects of feeding by four capitula feeding insects (i.e. weevils *B. orientalis* and *E. villosus* and picture winged flies *U. sirunaseva* and *C. succinea*). The action of the rosette weevil *C. basicorne* on YST via plant damage reduces resources for the other herbivores. The competitive interspecific interactions among the capitula feeders are direct (see Gutierrez et al. 2005) while their interaction with the rosette weevil are indirect via its effect on plant growth and survival and the reduction in capitula numbers and seed production.

The YST system model is composed of age-structured population dynamics models

(PBDMs) for whole plants, plant subunits (leaves, stem, root, and capitula), and for the different herbivores. Specifically, the YST system has 17 linked functional PBDMs {✗ = 1, …, 17} consisting of six linked population dynamics models for healthy plants: a canopy of an age-structured population of plants {✗ = 1} and linked subunit models for age-structured mass of leaves {✗ = 2}, stems {3} and roots {4}, and for age-structured populations of mass and numbers for capitula {5, 6} (Gutierrez *et al.,* 1993, 2005). The populations of the four seed feeders {7-10} are dynamically linked to their preferred stages of capitula {5, 6} and reduce seed production in infested capitula at rates dependent on the infestation level (see Gutierrez et al., 2005). *C. basicorne* {11} larvae attack rosette stage plants that continue development at a reduced rate (Smith 2006) and produce fewer seed at maturity (Uygur et al. 2005). In the model, YST plants (and their subunits) attacked by *C. basicorne* are transferred from {1-6} to the same stage and age classes in separate dynamics models (e.g., {12-17}) where they are followed to assess the impact of larval feeding on their development and growth.

The parameters for YST and the four capitula feeding herbivores {1-10} were summarized in Gutierrez et al. (2005) and are not reviewed here, while the parameters for the rosette weevil {11} are given in Table 1. The initial conditions for the models at all locations in this study are 3500 YST seed m^{-2} and 10 adult m^{-2} of each herbivore species. The YST system model is modular allowing any combination of species to be included using simple true-false Boolean instructions from a batch run file.

Thermal biology

Yellow starthistle and its insect natural enemies are heterothermic, and hence aging and all biological rates in the model are in physiological time units (degree-days, *dd*) above the respective temperature threshold of each species. Data were not available to fully characterize the rate of development on temperature, and hence we used the linear day degree model to estimate developmental times. The half sine method of Gilbert et al. (1976) is used to compute daily increments of *dd*. The lower developmental threshold for yellow starthistle is 8ºC, and that for the seed feeding herbivores which become active in spring is 9ºC (see Gutierrez et al. 2005). Because the rosette weevil is active in early spring, its lower and upper thermal thresholds are assumed to be relatively low; 6.5°and 28.5°C respectively. The developmental times of the rosette weevil life stages computed at 19°C are: egg (94*dd*), larvae (635*dd*), pupae (235*dd*), adult pre-reproductive period (90 *dd*) and the reproductive period is 650*dd* (estimated from Smith and Drew 2006). The time step in the model is a day of variable length in physiological time above the thermal threshold of each of the species. Only 25% of hibernating weevil adults is assumed to return and become active during spring to feed and oviposit on rosette plants.

2.3 The bio-demographic functions for YST

The modeling paradigm assumes that all organisms search for resources to meet demands that vary with weather conditions and their current stage and age. In the model, the same predator form of the resource acquisition model recurs for different resource acquisition processes (e.g., eqn. 1; see Gutierrez 1996).

Ignoring the time variable *t* (i.e., day), the daily photosynthesis rate is strongly influenced by weather (see Gutierrez et al. 2005). Briefly, the photosynthetic rate (*S*) of YST plants per m^2 is:

$$S = f(\cdot) = \phi_w D(1 - e^{-a\phi_g E/D}), \qquad [1]$$

where *D=D(T)* is the maximum average demand at temperature *T* by all plants at their current stage and mass*;* $a = 0.86$ is the proportion of light intercepted (i.e., the search rate); $E = cal\ m^{-2}/3.875$ is the light energy incident in the m^2 converted to gram dry matter; $0 \le \phi_w = (S_w / D_w) < 1$ scales for the effect of water (*w*) shortfalls on *S* where $S_w = D_w(1 - e^{-a_w w/D_w})$ is the water uptake rate, D_w is the demand for water and a_w is the root search rate; competition from grasses for light is $0 \le \phi_g = e^{-0.5LAI_g} < 0.1$ where LAI_g is the leaf area index for grass. The ratio 0<*S/D*<1 from eqn. 1 is the proportion of the photosynthate demand met and is used to scale the maximum rates of plant growth and fruit production (numbers and mass). The daily soil water balance is computed using a biophysical model (Ritchie 1972) altered to our supply-demand paradigm (see Gutierrez et al. 2005).

Mortality in YST is most severe in the cotyledon and seedling stages due to intraspecific competition and shortfall in *S/D*. As survivorship terms, the two factors are captured by eqn. 2 as

$$0 < lx_{comp} = \left(S/D\right)_{avg} e^{-0.065(\text{cotyledon+seedlings})} \le 1, \qquad [2]$$

where $(S/D)_{avg}$ is the running seven day average of the *S/D* ratio. Fungal disease affects survivorship of cotyledon and seedling stage plants in high rainfall areas and is included in the model as a function of mm rain:

$$0 < lx_{disease} = e^{-0.015 rain} \leq 1. \qquad [3]$$

In the model, YST is assumed to succumb to temperatures below -8°C. Hence survivorship of the cotyledon and seedling stages due to these factors at time *t* is the product $lx_{comp} lx_{disease} lx_{T<-8C}$.

Attack by the rosette weevil reduces seed production and plant growth rates. In attacked plants, photosynthesis (*S*, eqn. 1) is reduced by weevil feeding (i.e. eqn. 4) and is expressed via the scalar ratio 0<*S/D*<1 on plant subunit growth and bud production rates of approximately 14% per larvae per plant (see discussion).

$$S = f(\cdot)(1 - e^{-0.15\ larvae/plant}) \qquad [4]$$

In addition, seed production in infested plants at the end of the season is reduced 7.25% per new adult produced per attacked plant.

Between seasons survival of seed enables YST to survive drought years, and in the absence of definitive field data, we assume 50% of the seed in the soil (B_{soil}) is depleted each year (*y*). At this rate, only $0.5^5 \times 100 = 3\%$ of a year's cohort of seed (*seed(y)*) survives five years. At the end of each season, the seed bank for the next year ($B_{soil}(y+1)$) consists of surviving seed from prior years ($0.5\ B_{soil}(y)$) and the current year's seed production (*seed(y)*). The yearly balance is computed as $B_{soil}(y+1) = 0.5\ B_{soil}(y) + seed(y)$ with the seed density declining when $0.5\ B_{soil}(y) > seed(y)$.

Daily seed germination within the season depends on the initial available seed ($B(y,t_0) = 0.5\ B_{soil}(y)$), the time and amount of rainfall and temperature via a symmetrical concave function ($0 \leq \phi_G(T) \leq 1$) that scales germination in the range 8°C to 28°C. Ignoring the year variable *y*, the number of seed that germinate ($B_G(t)$) at time *t* (day) during the season is

$$B_G(t)=\phi(T)B(t)(1.0-e^{-0.04\,rain(t)})\ ,\qquad [5]$$

and $B(t+1)=B(t)-B_G(t)$.

The attack biology of the rosette weevil

In the model, we first compute the host plant finding success rate of adult females and then compute the total number of eggs deposited by the population. Weevil females are assumed to search randomly for host plants (Clement et al., 1989) with a maximum demand rate of one rosette plant per day. The number of plants attacked (*na*) by weevils at temperature T at time t (i.e., day) is computed using eqn. [6] where h is the number of healthy and previously attacked rosette plants m^{-2}, a_W= 0.8 is the weevil search rate (see discussion), w is the number of females m^{-2}, and $0\le\phi_T(T)\le 1$ is a symmetrical concave function that scales the search rate due to temperature in the range 6.5°C to 28°C. Ignoring the time variable t,

$$na(T,h,w)=w(1-e^{-a_w\phi_T(T)h/w}).\qquad [6]$$

The attacks (*na*) are apportioned as a proportion of healthy and attacked plants in the population.

The total number of eggs (*E(w,h,T)*) laid by all females *w* is computed using eqn. [7] assuming an average oviposition rate of 1.9 eggs day^{-1}♀$^{-1}$ at 19°C

$$E(T,h,w)=1.9\phi_T\phi_I na\ ,\qquad [7]$$

where $\phi_T(T)$ from eqn. [6] scales the reproductive potential for the effects of temperature and $0.5\le\phi_I=1.0-0.15\times(larvae\ +pupae+\ new\ adults)/\,attacked\ plants\le 1$ scales preference for the effect of plant deterioration due to prior attacks.

Weather data

Weather determines the dynamics, distribution and relative abundance of YST and its natural enemies at specific locations and in the aggregate on a larger regional scale. Daily max- min temperatures, solar radiation, rainfall and available soil moisture are the forcing variables for YST, while the herbivores are driven by temperature and host availability (i.e., capitula or rosette stage plants). Ambient weather data from the AgMERRA global weather dataset for the period of 1980-2010 were used. The AgMERRA dataset was created as a baseline forcing dataset for the Agricultural Model Inter-comparison and Improvement Project (AgMIP, http://www.agmip.org/, see Ruane et al. 2015), and is a daily time series of max-min temperatures, solar radiation, rainfall and RH at ~ 25 km geographic resolution (National Aeronautics and Space Administration 2015). AgMERRA incorporates the MERRA-Land dataset (Reichle et al. 2011) that provides substantial improvements in the resolution of daily precipitation distribution and precipitation extremes when compared to other climate forcing datasets (see Ruane et al. 2015). Daily weather data used are for 17,854 lattice cells across Europe, the Mediterranean Basin, Eurasia and North Africa and 5,649 lattice cells across the western United States (states CA, AZ, NM, CO, UT, NV, ID, OR, WA, MT, WY). The lattice cells are about 25 × 25 km.

Simulation studies and GIS mapping

Using the YST system model, we first examined roles of weather and natural enemies on the geographic distribution and relative abundance of YST at three locations in Turkey and then regionally across its known range in the Mediterranean Basin. We then used the model to explore the potential for the biological control of YST in the Western USA. Simulations for all lattice cells begin on 1 January 1980 using the same initial conditions and run continuously on a daily basis (see above; table 1). Selected annual summary variables were georeferenced and appended by year to a text file for GIS mapping and statistical analysis. The open source GIS software GRASS version 6.4 maintained by the GRASS Development Team (2014) was used to map the simulation results using 3 point bi-cubic spline interpolation on a 3 km raster grid. The geographic patterns in the maps reflect local site favorability and geographic distribution. (*n.b.*) While the model includes detailed biology, PBDMs are not one-to-one descriptions of nature, and hence the predictions of the YST system model are prospective and must be viewed as relative in nature.

RESULTS

Site specific dynamics in Turkey - For heuristic purposes, we simulated the system dynamics at two locations in Turkey (Fig. 1c) having very different climates for the period 1990-2010: Inebolu on the Black Sea coast, and Kayseri in central Turkey. We first simulated the dynamics of YST without herbivory to gauge the suitability of weather at the locations for YST (see supplemental materials; SM), and then the added effects of *B. orientalis*, *E. villosus*, *C. succinea*, *U. sirunaseva* and *C. basicorne* on YST's distribution and relative abundance (see text). We also examined the dynamics for Adana in the south Mediterranean area near NW Syria, but report the results in the supplemental materials.

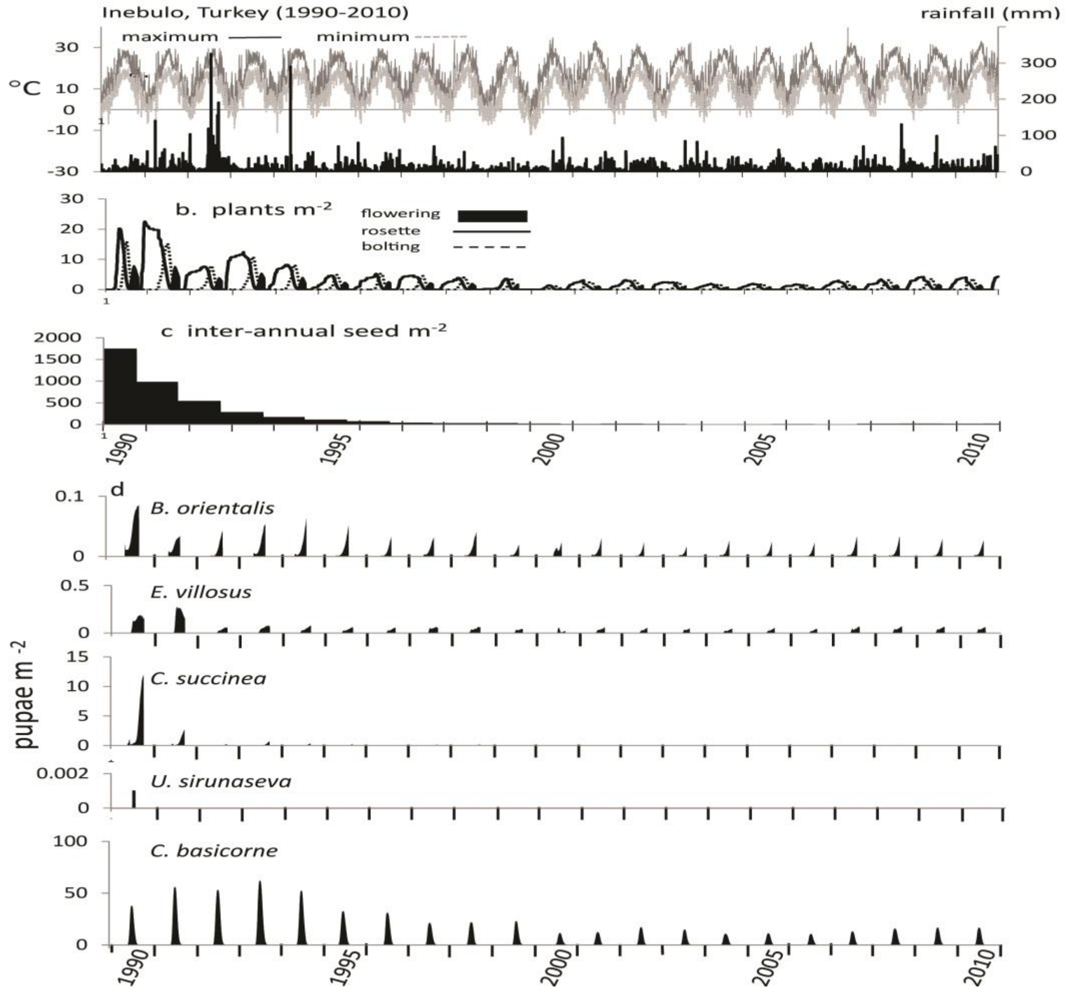

Figure 2. Simulated prospective dynamics of YST stages during 1990-2010 at Inebolu, Turkey on the Black Sea coast with five natural enemies: (a) max-min temperature and daily rainfall, (b) dynamics of the rosette, bolting and flowering stages of YST, (c) seed bank densities, and (d) the pupal dynamics of *B. orientalis*, *E. villosus*, *C. succinea* and *U. sirunaseva* and *C. basicorne.*

Inebolu, Turkey – Observed daily rainfall and max-min temperatures for the period 1990-2010 are presented in Fig. 2a.

In the absence of herbivory, seed pool densities ranged from 2000-5000 m^{-2} (see supplemental materials Fig. SM1a), the densities of cotyledon and seedling stage plants were at times greater than 1000 m^{-2}, while the population of flowering plants m^{-2} varied prospectively from 250 to 320 m^{-2} (Fig. SM1b). The dynamics reflect the timing and quantity of rainfall on germination, the effects of crowding on mortality of cotyledon and seedling stages (eqn. 2), and mortality due to disease (eqn. 3) (see Gutierrez et al. 2005). The dynamics of capitula numbers and leaf drymatter are illustrated in Figs. SM1c-d.

In the presence of the five herbivores, mature flowering plant density declined from about 250 plants m^{-2} to ~2 m^{-2} after four seasons (Fig. 2b) with seed pool densities decreasing >95% to near zero (Fig. 2c). Years 1998 and 1999 were cold and caused mortality of fall germinating YST. The pupal dynamics of the five herbivores are depicted in Fig. 2d with only *C. basicorne* >> *E. villosus* > *B. orientalis* producing consistent annual populations. Predicted populations of the picture wing flies *C. succinea* and *U. sirunaseva* were very low. *C. basicorne* populations peak at about 60 pupae m^{-2} and stabilized at about 5 pupae m^{-2} in later years.

Kayseri, Turkey – In the absence of herbivory, seed pool densities ranged from 200-3500 m^{-2} (supplemental materials Fig. SM2), while the population of flowering plants m^{-2} varied greatly from near zero to 350 m^{-2} during the 2000 to 2010 period (Fig. SM2b). Compared to Inebulo, average season long rainfall at Kayseri was about 40-50% with rainfall events fluctuating widely (Fig. 2a vs. Fig. 3a), and total degree-days were about 8-10% lower (Fig. SM3). Rainfall was more variable than at Inebulo and this affected germination times and rates, the length of the season, vegetative growth rates and plant survival, the dynamics of capitula production, and seed production. In addition, freezing temperatures < -8°C were common during winter (Fig. 3a) and killed fall germinated YST. These factors caused the density of mature flowering plants to fluctuate considerably.

With the addition of the capitula feeding insects and the rosette weevil, plant densities were greatly reduced and fluctuated from 1 to 12 plants m^{-2} (Fig. 3b) and seed densities ranged from ~1800 to near zero (Fig. 3c). Herbivore dynamics were greatly influenced by plant growth dynamics and densities with only the rosette weevil developing consistent high populations with

C. basicorne >> *E. villosus* > *B. orientalis* > *C. succinea*.

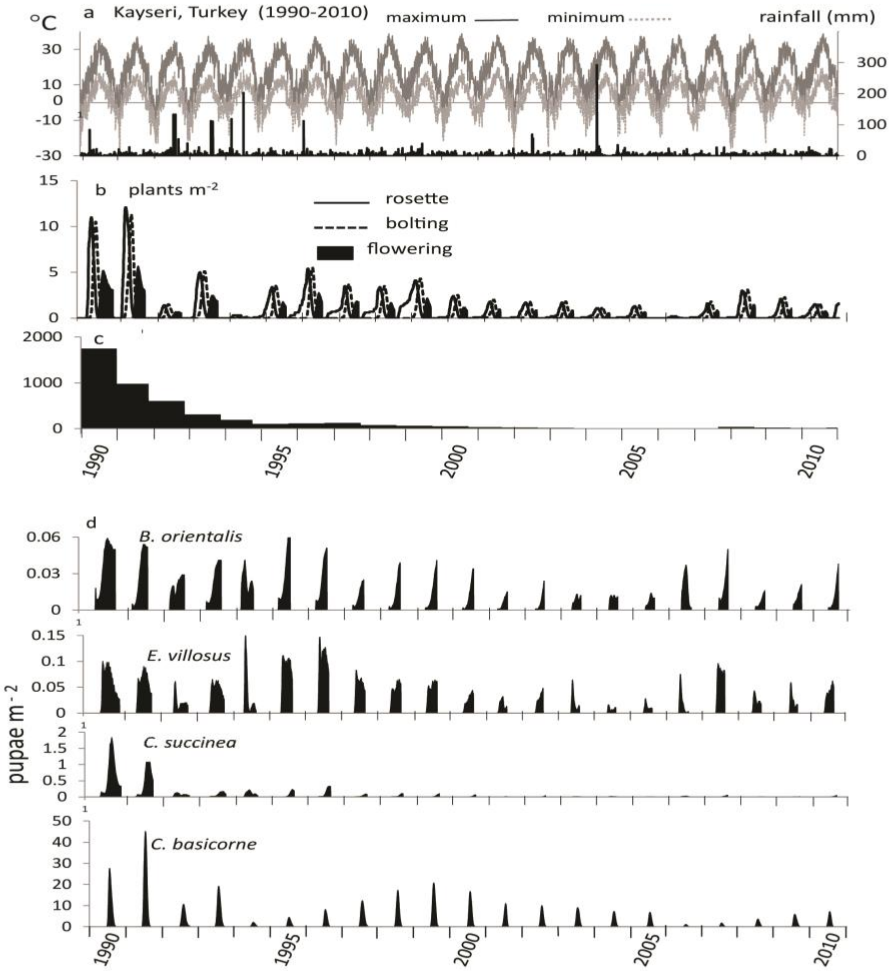

Figure 3. Simulated prospective dynamics of YST stages during 1990-2010 at Kayseri in Central Turkey with five natural enemies: (a) max-min temperature and daily rainfall, (b) dynamics of the rosette, bolting and flowering stages of YST, (c) seed bank densities, and (d) the pupal dynamics of *B. orientalis*, *E. villosus*, *C. succinea* and *U. sirunaseva* and *C. basicorne.*

Adana, Turkey – The climate of Adana is typically Mediterranean in character with rainfall occurring in fall through spring (Fig. SM4a) and temperatures rarely fall below 0°C. Only simulations including all five herbivores were made for this location. Flowering plant density fell rapidly from about 50 after three years to about two plants m^{-2} (Fig. SM4b) with inter annual seed pool declining to near zero (Fig. SM4c). Years 1997 and 1998 were dry and this greatly affected plant germination, survival, and seed production (Fig. SM4b, c). Because a cohort of seed germinates over several years, inter annual seed survival allows YST to survive dry years. Only *C. basicorne* >*E. villosus* >*B. orientalis* maintained low but discernible populations during the 1990-2010 period, with *C. basicorni* populations peaking at ~70 but declining in later years.

YST in the Mediterranean Basin, Europe and Eurasia

The potential relative abundance and dynamics of YST at each location is determined by local weather (see supplemental materials) with observed densities determined by the action of natural enemies (e.g., Figs. 2, 3).

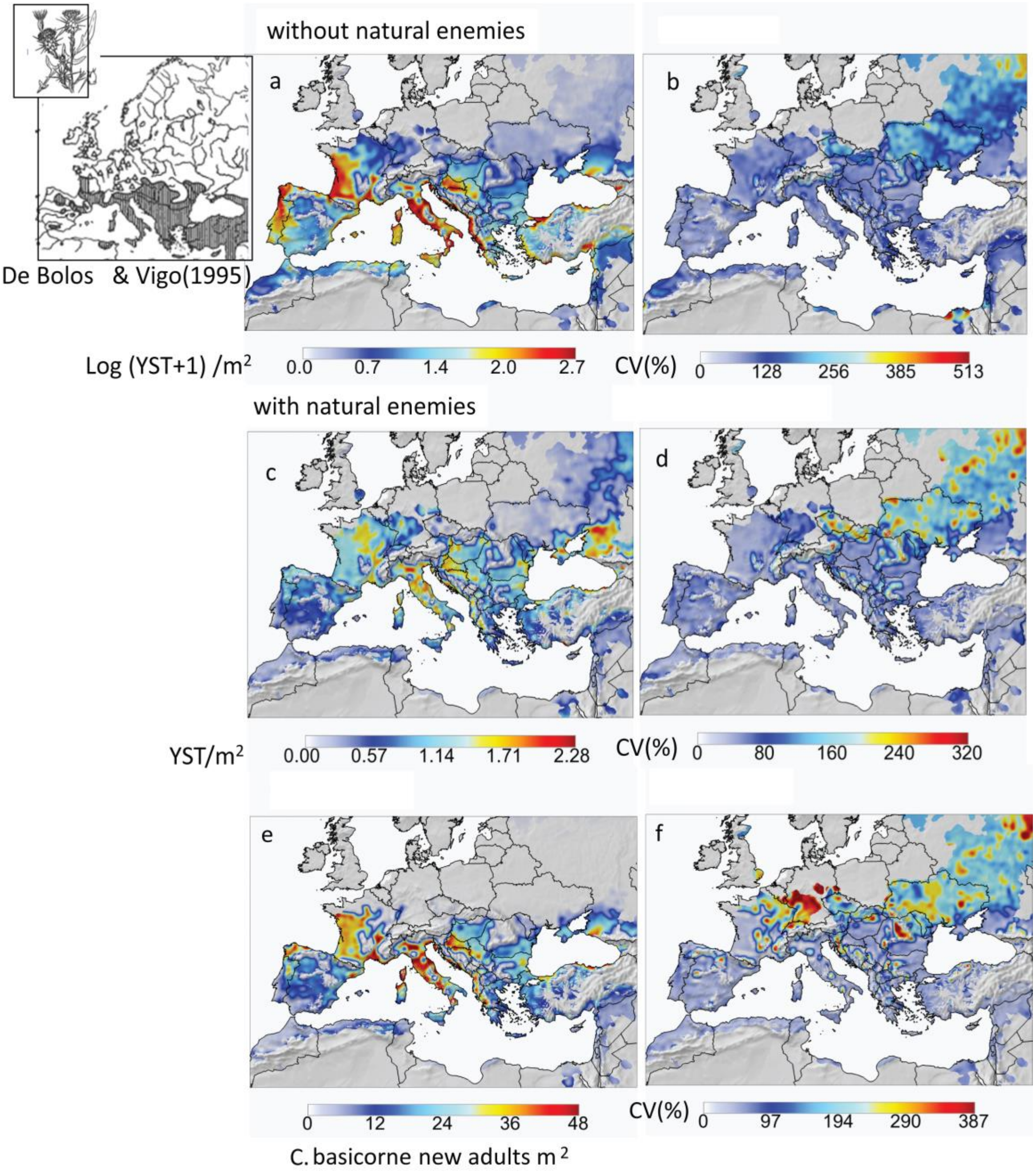

Figure 4. Simulated prospective average distribution and relative abundance of yellow starthistle (YST) in Europe, the Mediterranean Basin and Eurasia during 2000-2010 below 1500m elevation: (a) $\log_{10}$ mean density m^{-2} without natural enemies. (b) coefficient of variation for the untransformed data in 5a, and (c) mean density m^{-2} with all five natural enemies, (d) coefficient of variation, and (e) the geographic distribution and mean abundance of new *C. basicorne* adults m^{-2}, and (f) the coefficient of variation (CV(%)). The known distribution of YST (De Bolos and Vigo 1995) is shown in the upper left inset.

In the absence of natural enemies, we examine the favorability of weather for YST across the region. Prospective plant densities varied widely in the range 0 - 400 flowering plants m^{-2}, and to get a better representation of the distribution, the data were transformed as $\log_{10}(YST+1)$ (Fig. 4a). The CVs of the untransformed data are presented as percentage and range from ~0 to 536% (Fig. 4b). Favorability is highest in France, Italy and parts of Greece. Low YST densities are associated with high CVs and the two variates help define unfavorable areas. The distribution of YST predicted by the model without natural enemies is similar to the rough distribution of YST presented by De Bolos and Vigo (1995) (Fig. 4a inset).

Given the action of all five natural enemies, the prospective average geographic distribution and abundance of YST (Fig. 4c) was estimated after the system had equilibrated (see Figs. 2, 3) using the 1995-2010 subset of the data, with the associated CVs mapped in Fig. 4d. The range of predicted relative densities of YST varied in the range [0, 2.5] with the CV shown in Fig. 5f varying in the range [~0, 320%]. The geographic distribution of YST did not change with herbivory with values of $CV < 100$ helping define the distribution of relatively stable YST populations. The predicted geographic distribution and relative abundance of new rosette weevil adults (Fig. 4e) is roughly the same as for YST.

YST in the Western USA

In the absence of natural enemies, the prospective average YST densities during 1995 – 2010 across the western USA ranged from [0, $110m^{-2}$], but to better illustrate the distribution of relative abundance, the data are again mapped as $\log_{10}(YST + 1)$ (Fig. 5a). The CVs of the untransformed values are mapped in Fig 5b (range [0, 423%]). Low populations are predicted in many areas of the western USA, intermediate densities are predicted in many areas of California, SE Washington and western Idaho, with highest populations in areas of high rainfall in Northern California, western Oregon and Washington and in the mountainous areas of central Arizona. The model does not include competition from woody perennial shrubs and trees, and this explains the predicted high YST abundance in higher rainfall areas. The highest predicted densities in the western USA are less than 1/3th those predicted in the more favorable areas of the Mediterranean Basin in the absence of natural enemies. The predicted low YST densities in much of the southwestern USA is due to the dry hot summers common in much of the region; weather that is similar to areas of North Africa and Spain. Late summer North American monsoon rains occur during wet years in southern areas of Arizona and New Mexico but this rain would be insufficient for YST to produce seed the following summer. As in the Mediterranean Basin, low YST densities are associated with high CV, and in the western USA, CVs < 100% again help define areas of high favorability (Fig. 5b).

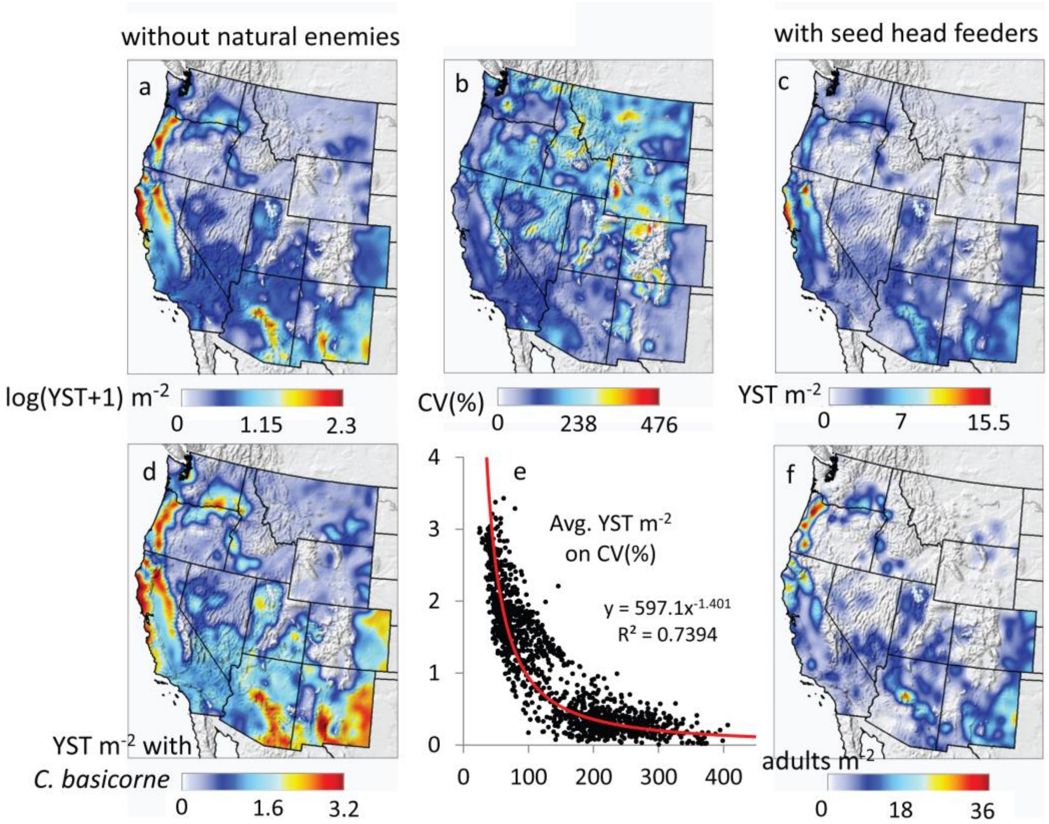

Figure 5. Simulated prospective average distribution and relative abundance of YST m^{-2} in the western USA during 1995 – 2010: (a) prospective log(YST+1) density without the capitula feeding natural enemies, (b) the CV(%) of data in Fig. 5a, (c) YST density with the capitula feeding natural enemies (*B. orientalis*, *E. villosus*, *C. succinea*, *U. sirunaseva*), (d) average YST density with the addition of *C. basicorne* to Fig. 5c, (e) a plot of YST density in Fig. 5d on the CV(%), and (f) the distribution of average new adult *C. basicorne*.

Including herbivory by the four established capitula feeding herbivores reduced prospective average abundance of YST [range ~0, 15.5 m^{-2}] (Fig. 5c), but the geographic distribution was unchanged. Depending on location, the capitula feeding insects reduced average density by about 60%. This prediction contrastd with an average reduction of 20-30% predicted by the version of the YST model reported by Gutierrez et al. (2005) for California using 1980-1990 weather. The highest YST densities were again predicted in higher rainfall areas of northern California and western areas of Oregon and Washington. The map also predicted high infestations in some areas of central Arizona and southeastern New Mexico.

The addition of the rosette weevil (*C. basicorne*) to the system reduced average relative YST density a further ~60% to a range of [~0, 3.2 m^{-2}], and changed the apparent distribution of YST (Fig. 5c vs. 5d) as high populations declined more than low populations. Predicted YST density was negatively related to CV as a percentage (Fig. 5e; $YST = 597.2\ CV^{-1.401}$, $R^2 = 0.74$). The prospective distribution and abundance of *C. basicorne* is illustrated in Fig. 5f with highest population densities in areas of high YST densities (Fig. 5c).

Analysis of simulation data for the western USA – Four simulation studies were made for the 1980-2010 period for all sites in the Western USA: (1) YST without natural enemies, (2) with capitula insects, (3) with capitula insects and the rosette weevil, and (4) with only the rosette weevil. Linear multiple linear regression analysis was performed only on the data for the 1980-1995 period of rapid decline in YST density due to herbivory. Prediction as measured by explained variance was not the goal, rather we sought to estimate the relative effects on $\log_e$ mature YST plant density across the region of abiotic factors (*dd* (degree days) and mm rainfall) and biotic factors (i.e. capitula feeding herbivores as a group and of the rosette weevil). The competitive effects of grasses and the individual species of capitula herbivores and their interactions in control of YST were analyzed by Gutierrez et al. (2005) and are not discussed here. The inclusion of the capitula feeding species as a group ($x_{Ev,Bo,Us,Cs}$) and of the rosette weevil (x_{Cb}) were represented in the data as presence - absence values (1, 0 respectively) (eqn. [8]). Only independent variables having significant *t*-values (p<0.05) were retained in the regression, and their average values and t-values are given in parentheses below. The average of 0.5 for presence-absence for $x_{Ev,Bo,Us,Cs}$ and x_{Cb} accrues because only half the runs included either variable, while a value of 0.25 for the interaction term implies that only a quarter of the runs included both.

$$\ln YST = 0.277 + 0.000320dd - 0.000411rain - 0.391x_{Ev,Bo,Us,Cs} - 0.484x_{Cb} + 0.187x_{Ev,Bo,Us,Cs}x_{Cb}$$

$$R^2 = 0.087,\ df = 39{,}102,\ F = 744.77 \qquad [8]$$

$$\textit{abiotic factors}:\ dd\ (avg = 2899,\ t = 49.00),\ rain\ (369.5,\ -35.495),$$
$$\textit{biotic factors}:\ x_{ev,Bo,Us,Cs}(0.5,\ -17.00),\ x_{Cb}\ (0.5,\ -21.09),\ x_{ev,Bo,Us,Cs}x_{Cb}\ (0.25,\ 5.75)$$

Taking the antilog of eqn. 8, we get

$$YST = 1.320e^{0.000320dd - 0.000411rain\ - 0.391x_{Ev,Bo.Us,Cs} - 0.484x_{Cb} + 0.187x_{Ev,Bo.Us,Cs}x_{Cb}}\ .$$

Positive exponents in eqn. 8 are for factors that increase YST population density while those with negative values decrease it. Temperatures are generally not limiting throughout the range of YST in the western USA, and the regression coefficient for *dd* is positive. In the aggregate, the coefficient for rainfall is negative because it affects several components of YST biology; the time and rate of germination, seedling fungal mortality, and the growth rates of plants that at higher levels increase resources for herbivorous natural enemies (see Figs. 2, 3). YST m^{-2} is negatively correlated to the presence of *C. basicorne* and the capitula feeding insects, but it is positively correlated to their interaction which is a measure of the effects of herbivore interspecific competition. The full analysis is in Fig. SM5.

To interpret eqn. 8, we first use average values for *dd* and mm rainfall and herbivore presence-absence (i.e., 0.5). Compared to no natural enemies, the average net action of all natural enemies reduced average YST density 32.24% to 1.94 m^{-2}. To examine the action of the capitula feeding herbivores alone, we set $x_{Ev,Bo,Us,Cs}$ equal to 1 and x_{Cb} equal to 0 resulting in a 32.3% reduction in YST density compared to no insects. Similarly we examine the effect of x_{Cb} =1 and $x_{Ev,Bo,Us,Cs}$ = 0 and observe a 38.43% reduction. Last, the combined action of all herbivores ($x_{Ev,Bo,Us,Cs}$=1, x_{Cb}=1) including the interaction reduced YST by 49.7%. However, a comparison of highest densities in more the favorable areas illustrated in Fig. 5a vs. 5c showed that YST densities were reduced > 80% by capitula feeding insects compared to no insects, while adding x_{Cb} reduced YST densities a further ~80% (Fig. 5c vs. 5d).

The effect of rainfall was illustrated as follows: areas of predicted high YST had more than 600mm of annual rainfall and the combined reduction of YST by $x_{Ev,Bo,Us,Cs}$, x_{Cb} and rainfall was 54.2%, but it was 61.1% at 1000mm, and 68.4% at 1500mm. These results show the average modulating influence of rainfall on the impact of natural enemies on prospective YST densities. The 300 and 500 mm rain isohyets are shown in supplemental materials Figs. SM6a, b. The predicted distribution of YST in Western USA (Fig. 5a) is above the 300mm isohyet.

DISCUSSION

How to assess the potential impact of prospective natural enemies for release across large areas with different climates and in the face of climate change remains elusive (e.g., Gutierrez et al. 2001; Gerard et al. 2013, Selvaraj et al. 2013). Section 4.3 ("Assumptions about future trends") by Working Group II in the fourth assessment report (AR4) of IPCC (IPCC 2014) outlines the shortcomings of widely used standard methods used to predict the geographic distribution of invasive species that are based largely on the climate envelope approaches (i.e., ecological niche models, ENMs). Among the gaps identified in IPCC AR4 were the "inability to account for species interactions, the lack of physiological mechanisms, and the inability to account for population processes" (IPCC 2014). IPCC AR5 in Section 4.5 ("Emerging issues and key uncertainties") stated insufficient knowledge about the "consequences for species interactions of differing […] responses to climate change and […] referred to "the inherent complexity of ecosystems" as a major source of uncertainty in predicting the response of terrestrial ecosystems to climate change (IPCC 2014). While the IPCC reports focused on climate change, the same short comings are evident in the analysis of extant weather on the potential impact of prospective natural enemies when introduced to new areas (see Guisan et al. 2014).

The use of physiologically based models circumvents some of the shortcoming of ENM approaches (Gutierrez & Baumgärtner 1984; Gutierrez et al. 2010) as shown here for the YST (*C. solstitialis*) system. The YST system model, albeit incomplete, is a mechanistic summary of the available data on the biology of YST and five of its herbivores, each of which responds differently to weather and each other across their wide geographic range. Because weather is the major driver of the system, the PBDM approach also lends itself to studies of the potential effects of ongoing climate change on YST (Gutierrez et al. 2010, 2010; Gutierrez and Ponti 2014).

Prospective impact of the rosette weevil

Our analysis sought to capture the weather-driven population biology of YST and five herbivorous natural enemies in its area of origin (the Mediterranean Basin and Eurasia), and then to evaluate the potential benefits of the introduction of the rosette weevil (*C. basicorne*) for the biological control of YST in the western United States where it is a serious nuisance in many areas. Weather (i.e. temperature, rainfall and solar radiation) drive the phenology and population dynamics of yellow starthistle and via plant bottom up effects greatly influences the dynamics of herbivores attacking it. For example, YST may be more abundant and grows larger during wet years (Sheley & Larson 1994; Morghan & Rice 2006), but this may provide higher levels of resource for natural enemies (see supplemental materials Fig. SM1d). In wetter areas (e.g., Inebolu on the Black Sea coast; Fig. 2), high rainfall increased plant disease mortality to seeds and emerging plants. In areas with low but highly variable rainfall such as Kayseri in central Turkey, the dynamics of YST varied greatly in response and this affected its natural enemies (Fig. 3). Natural enemies reduced within season growth and reproduction and the carryover of seed between seasons.

Prior studies showed that capitula-feeding natural enemies introduced to the USA for the biological control of YST are generally ineffective because of seed production in uninfested capitula, high survival of seed in attacked capitula, and because YST compensates by producing larger plants with more capitula at reduced plant densities (Gutierrez et al. 2005; Garren and Strauss 2009; Swope and Parker 2010). At some locations in California with high natural enemy densities and competitive grass populations, YST densities have gradually decreased (Pitcairn et al. 2005; Woods et al. 2007). However, an experimental field study failed to show population-level impact of capitula insects on YST population density (Garren and Strauss 2009). Mowing experiments reduced YST growth and reproduction more than herbivore bud damage alone (Spencer et al. 2014). Modeling analysis by Gutierrez et al (2005) suggested that biological control agents that kill whole plants and/or greatly reduce seed production in surviving attacked plants are required for control of YST. The rosette weevil has some of these attributes, but it has not been introduced to North America because of host specificity concerns (Hinz et al. 2014). Simulation studies here suggest that in the absence of natural enemies, areas of the Mediterranean region are 3 fold more favorable for YST than favorable areas of the Western

USA, and yet the observed densities of mature plants in Turkey are about 4% those in California (Uygur et al. 2012).

On first observation, the biology of the rosette weevil suggests that it would not be an efficient natural enemy of YST as it attacks only rosette stage plants, it is univoltine, adult fecundity is low (< 2 eggs/day at 19°C), and egg survivorship is <30%. However, the adults are long lived (Smith and Drew 2006), and the larvae burrow into the root crown reducing plant vigor that reduces plant growth and seed production. In Turkey, up to seven *C. basicorne* larvae were found in YST roots and average seed viability was reduced (Uygur et al. 2005). Greenhouse experiments show that 4.2 ± 3.0 larvae per plant caused 23% reduction in the size of well-watered, fertilized potted plants (Smith 2006), and likely had a similar or even greater effect on seed production and viability. Under field conditions, the effect is likely to be greater where water stress may be a factor (e.g., Klamath weed; Huffaker and Kennett 1959).

The model assumes a homogenous environment, but in the field the environment may be heterogeneous with microhabitats occurring in arid regions where water may accumulate and provide favorable habitat for the development of YST and its herbivores. However, to model this would require the development of a meta-population system model and detailed information about the distribution and favorability of these habitats, and the rules of movement of the herbivores between them (see Gutierrez et al. 1999).

The YST system model was designed to demonstrate the relative effects of *C. basicorne* attack and not to make precise predictions. In the model, feeding by the rosette weevil reduced the photosynthetic rate, decreased growth and flower head production, and seed yield in attacked plants. Varying the reduction in photosynthetic rate per infesting larvae per plant to simulate this effect on attacked plants, and as expected lower levels of physiological damage allowed increasingly more plants to achieve higher seed production rates reducing the impact of *C. basicorne* beyond that caused by the capitula feeding insects. A value of 0.075 in eqn. 4 for the coefficient that scales the photosynthetic rate for weevil damage yielded maximum plant densities of 3.4, while a value of 0.15 yielded densities of 3.2. Both values result in > 60% reduction in YST densities (Figs. 2-4).

The search parameter (a_w) for *C. basicorne* in eqn. 6 is not known, but field observations suggest that the weevil is able to find plants when densities are low. The model is robust to changes in the search parameter in the range $[0.15<a_w<1.0]$ that affects weevil attack rates with low values slowing the control of YST. A value of unity for a_w makes search success a purely random process, while lower values make search success less than random. In the model we used a value of 0.8.

Because of the rosette weevil's mode of action, our heuristic analysis suggests *C. basicorne* could have significant additional impact on YST in the Western USA, and depending on rainfall levels could possibly reduce YST densities an additional 25-70% across the western USA above that of established capitula feeding insects (eqn. 8).

Introduction of the rosette weevil to North America

Approval for the release of the rosette weevil in the USA has not been granted because of concerns about possible risk to safflower crops (*Carthamus tinctorius*) and the ornamental cornflower (*Centaurea cyanus*) that are of Palearctic origin (Smith 2006, Hinz et al. 2014, L. Smith pers. comm.). Recent studies on *C. basicorne* suggest it is more host specific than suggested initially by Clement et al. (1989) in Italy. For example, during a three year study in Eastern Turkey, Smith et al. (2006) assessed the risk of *C. basicorne* to safflower in the field, and found that no safflower plants were attacked despite 48–100% attack rates on yellow starthistle. In no choice laboratory tests, Smith (2007) found the highest rates of successful larval development of *C. basicorne* on yellow starthistle and cornflower, but some development also occurred on closely related weeds such as *Centaurea melitensis* (Napa starthistle), *Cnicus benedictus* (blessed thistle), *Crupina vulgaris* (common *crupina*) and on safflower. Laboratory choice experiments showed strong preference for YST, moderate preference for cornflower and low preference for safflower (Smith 2012). Cristofaro et al. (2013) made releases of *C. basicorne* in a field experiment in Italy to evaluate the potential risk to two varieties of safflower grown in solid blocks flanking a central row of YST. They found that 54% of the YST but none of the 1021 safflower plants were attacked by the weevil. In addition, Rector et al. (2010) in a field experiment in France found that *C. basicorne* attacked yellow starthistle and cornflower but not safflower (see also Antonini et al. 2009). The rosette weevil is not known to attack safflower in its Palearctic range (Alonso-Zarazaga 1990, Wanat 1994), and host specificity data suggest that *C. basicorne* is highly stenophagous (Smith 2006).

Potential economic and environmental gains - YST is toxic to horses, infestations adversely affect native plants, affect wild life, and reduce the value of the land for grazing and recreational purposes (e.g., Maddox and Mayfield 1985). More than 5.7 million hectares are infested in California (Pitcairn et al. 2006), and millions more are infested across the western USA (see Maddox and Mayfield 1985). Currently, chemical and cultural controls are used to suppress YST populations, but they are costly and often cannot be implemented across a wide landscape (DiTomaso et al. 2006). Biological control of YST would result in considerable economic and environmental gains.

Eagle et al. (2007) estimated the total losses of livestock forage value due to YST on private land in the state of California at $7.65 million per year with control costs of $9.45 million per year. Together, these amount to the equivalent of 6%–7% of the total annual harvested pasture value for the state. In Idaho, Juliá et al. (2007) estimated annual costs of $12.7 million, with agricultural related economic impacts accounting for 79% of this total cost, and a non-agricultural impact of 21%. While the losses due to YST seem low given the pervasiveness of the weed in California, Eagle et al. (2007) posit this is due to the fact that YST tends to invade semi-arid grasslands typically having relatively low per-acre returns. Thus, while the relative impact on ranchers affected by YST may be large, the aggregate monetary losses due to reduced forage may be lower than that due other non-native weeds that invade more productive agricultural lands. However, Eagle et al. (2007) cautioned that the monetary values of YST on recreation and real estate are likely to be greater than on pastoral areas. Jetter et al. (2003) estimated that direct economic impact of yellow starthistle in California alone is between $40 million and $1.4 billion, depending on assumptions. On the positive side, YST is pollinated by some wild and domestic bees, and is considered to benefit some beekeepers (Goltz 1999, McIver et al. 2009, Leong et al. 2014).

Climate change effects

The spread of YST may increase with time and with climate change with unknown ecological and economic impacts (Bradley et al. 2009; Diffenbaugh et al. 2015). Eriksen et al. (2012) posit that local morphological and phenological adaptations may play a role in the success of *C. solstitialis* as an invasive weed in newly invaded areas. Furthermore, climate change may exacerbate the problem in North America as YST grows more than six times larger in response to elevated [CO_2] and more than three times larger in response to increased aerial nitrate deposition than other resident plants that respond less strongly or not at all to these changes (Dukes et al. 2010). This suggests that ongoing environmental and climate changes may dramatically increase the severity of YST infestations and possibly other weeds in western North America and elsewhere.

Epilogue

The model was designed to give insights to the rosette weevil's (*C. basicorne*) potential for control of yellow starthistle in Western North America, and not to give precise prediction across the wide geographic range of the weed. In total, the introduction of *C. basicorne* for the biological control of YST in the western USA would appear to be beneficial given the likely expansion of YST's range, growth and pest status in response to climate change (Dukes et al. 2010), its stenophagous feeding behavior (Smith 2006), and the weevil's potential for providing substantial increases in control.

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Images of the various species in Fig. 1 were copied from open sources on the internet.

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Table 1. Parameters for the *Ceratapion basicorne* submodel (Smith and Drew 2006; see Gutierrez et al. 2005 for the other species)

Biological parameters	
Egg stage	94.0 dd$_{>6.5^\circ\mathrm{C}}$
Larval stage	635.0 dd$_{>6.5^\circ\mathrm{C}}$
Pupal stage	235.0 dd$_{>6.5^\circ\mathrm{C}}$
Adult reproductive adult stage	650 - 900 dd$_{>6.5^\circ\mathrm{C}}$

New adult pre-reproductive period	90.0 $dd_{>6.5°C}$
Lower and upper thermal limits	6.5 to 28.0°C
Erlang parameter k	50 for each life stage
Aestivating adults	assumed not to age
Proportion of returning aestivating adults	0.25 (after January 1)
Egg survival	0.3
Plants attacked per female per day at 19°C	1
Per capita fecundity/day	1.9 eggs d^{-1}
Sex ratio	0.5
Rosette ages attacked (age from germination)	220 - 550$dd_{>8°C}$
Beginning of attack	when first rosettes available
Background immigration rate	0.0001 adult m^2/day
Intrinsic adult survivorship per day	$\max\{0.001,\ 0.0025 dda > 6.95^{\circ} C\}$
Reduction in photosynthesis, growth rates & bud production rates	$\max\{0.0,\ 0.0725 \times larvae / attacked\ plant\}$
Reduction in seed production per year	0.5

Initial conditions

10 hibernating rosette weevil adults m^{-2}

3500 YST seed m^{-2}

Appendix –Population dynamics model

The basic premise of the PBDM approach is that all organisms, including humans, face the same problems of resource (energy) acquisition and allocation (Gutierrez 1996; Regev et al. 1998; Gutierrez and Regev 2004). The model assumes energy allocation priority, first to respiration, then to reproduction and, if assimilate (revenues) remains, to growth (infrastructure costs). The shapes of the acquisition functions and maintenance costs are similar with the net being the amount of resources available for allocation to reproduction and growth. These analogies allow use of the same modeling structure to describe the dynamics of all interacting species. While the units and interpretation of the flow rates differ among species, this paradigm simplifies model development and allows assessment of plant growth and compensation in the face of herbivore damage.

The dynamics model

The Manetsch (1976)–Vansickle (1977) distributed maturation time population dynamics model is used for each of the 17 linked populations in our analysis (see text; and is implemented in discrete form (see Gutierrez 1996). Furthermore, the distribution of developmental times of cohort members in each population initiated at time *t,* have a characteristic mean and variance. Using the notation of DiCola et al. (1999, p 523-524), the general model for all species is characterized by assumption that the flow rates between age classes is regulated by ($v_i(t)$).

$$v_i(t) = v(t) = \frac{k}{del(t)}\Delta a \qquad i = 1,\dots, k \qquad \text{(A1.1)}$$

where *k* is the number of age intervals, *del(t)* is the expected mean developmental time and Δa is an increment in physiological age . From (A1.1) we obtain

$$\frac{dN_i}{dt} = \frac{k}{del(t)}[N_{i-1}(t) - N_i(t)] - \mu_i(t)N_i(t) \qquad \text{(A1.2)}$$

where N_i is the density in the *i*th age class and $\mu_i(t)$ is the proportional net loss rate due to all factors in the i^{th} age class.

In terms of flux $r_i(t) = N_i(t)v_i(t)$, yields

$$\frac{d}{dt}\left[\frac{del(t)}{k} r_i(t)\right] = r_{i-1}(t) - r_i(t) - \frac{del(t)}{k}\mu_i(t)r_i(t) \;.. \qquad \text{(A1.3)}$$

Applications to yellow starthistle.

The YST system model is composed of age-structured population dynamics sub models (PBDMs) for whole plants, plant subunits (leaves, stem, root, and capitula) and of the different herbivores (eqn. A1.3). Specifically, the YST system has 17 linked *functional populations dynamics models* {$\boldsymbol{X}$ = 1, …, 11}: a canopy of age-structured population of plants {$\boldsymbol{X}$ =1} and linked sub models for the age-structured mass of leaves {$\boldsymbol{X}$ = 2}, stems {3} and roots {4}, and linked age-structured populations of mass and numbers for capitula {5, 6} (*cf.* Gutierrez *et al.,* 1993, 2005). The populations models for the seed feeders {7-10} are dynamically linked to their preferred stage of capitula {5, 6} (see Gutierrez et al., 2005), while *C. basicorne* {11} attacks the rosette stage but continues development.

Because cohorts of plants germinate at different times and each cohort has subunit populations associated it, the associated subunits must progress in concert with their parent cohort of plants and each subunit population also progresses along its own age axis. These subunit populations require a 2-dimensional distributed delay model. Seed heads have mass and age structure and each requires a 2-dimensional distributed delay model. The number of capitula of different ages and their preference by each of the four capitula feeding insects is used to estimate the number that may be attacked. For example, $\mu_{5,i}$ could be the attack rate of *ith* age capitula {✗ = 5, 6} by the seed head feeding insects (see Gutierrez et al. 2005 for details).

YST plants (and their subunits) attacked by *C. basicorne* (✗ =11) are transferred from {1-6} to the same stage and age class in separate dynamics models (e.g., {12-17}) where they are followed to assess the impact of larval feeding on their development and growth. *C. basicorne* larval feeding reduces the photosynthetic rate of attacked plants and hence the growth of the plants and its subunits as well as the rate of capitula bud initiation and final seed production (see text and Gutierrez et al. 2005). It is via this feeding mechanism that *C. basicorne* interacts with the capitula feeding herbivores, and how it reduces YST densities. Note that water shortfalls also affect photosynthesis, compounding the effects of the rosette weevil (see text).

Figure Headings

Figure1. The interaction of yellow starthistle (YST) and the five herbivorous natural enemies: (a) the life cycle of YST and the points of attack by the natural enemies, (b) the dry matter flow rates in YST and the points of impact of the natural enemies, and (c) an inset of a map of Turkey showing the north to south locations of Inebolu, Kayseri and Adana respectively (see text). In sub figure 1a, the outer dashed curved arrows indicate the annual cycle of YST, the open thick double ended arrows indicate herbivore-host plant interactions and the thin solid double arrow competition between YST and grasses. Interactions between the capitula feeding herbivores are direct competitive interactions (see Gutierrez et al. 2005), while the effect of the rosette weevil on them is indirect via reductions in photosynthesis and plant growth. All photos of the organisms in composite figure 1a are from free access sources on the web.

Figure 2. Simulated prospective dynamics of YST stages during 1990-2010 at Inebolu, Turkey

on the Black Sea coast with five natural enemies: (a) max-min temperature and daily rainfall, (b) dynamics of the rosette, bolting and flowering stages of YST, (c) seed bank densities, and (d) the pupal dynamics of *B. orientalis*, *E. villosus*, *C. succinea* and *U. sirunaseva* and *C. basicorne.*

Figure 3. Simulated prospective dynamics of YST stages during 1990-2010 at Kayseri in Central Turkey with five natural enemies: (a) max-min temperature and daily rainfall, (b) dynamics of the rosette, bolting and flowering stages of YST, (c) seed bank densities, and (d) the pupal dynamics of *B. orientalis*, *E. villosus*, *C. succinea* and *U. sirunaseva* and *C. basicorne.*

Figure 4. Simulated prospective average distribution and relative abundance of yellow starthistle (YST) in Europe, the Mediterranean Basin and Eurasia during 2000-2010: (a) $\log_{10}$mean density m^{-2} without natural enemies. (b) coefficient of variation for the untransformed data in 5a, and (c) mean density m^{-2} with all five natural enemies, (d) coefficient of variation, and (e) the geographic distribution and mean abundance of new *C. basicorne* adults m^{-2}, and (f) the coefficient of variation (CV(%)). The known distribution of YST (De Bolos and Vigo 1995) is shown in the upper left inset.

Figure 5. Simulated prospective average distribution and relative abundance of YST m^{-2} in the western USA during 1995 – 2010: (a) prospective log(YST+1) density without the capitula feeding natural enemies, (b) the CV(%) of data in Fig. 6a, (c) YST density with the capitula feeding natural enemies (*B. orientalis*, *E. villosus*, *C. succinea*, *U. sirunaseva*), (d) average YST density with the addition of *C. basicorne* to Fig. 5c, (e) a plot of YST density in Fig. 5d on the CV(%), and (f) the distribution of average new adult *C. basicorne*.