

1 **Is there reduction in disease and predispersal seed predation at the border of a host plant's**
2 **range? - field and herbarium studies of *Carex blanda***

3

4 **Helen M. Alexander¹**

5 **Sarah Price¹**

6 **Rhonda Houser²**

7 **Debra Finch¹**

8 **Michael Tourtellot¹**

9 ¹Department of Ecology and Evolutionary Biology, The University of Kansas, Lawrence, KS
10 66045 USA

11 ²University of Kansas Libraries, The University of Kansas, Lawrence, KS 66045 USA

12

13 Send correspondence to H. Alexander, Department of Ecology and Evolutionary Biology,

14 University of Kansas, Lawrence, KS 66045 USA, halexander@ku.edu, FAX 785-864-5321

15

16 Running headline: Disease in peripheral host populations

1Summary

21. Small, isolated populations at species' borders have been postulated to be less likely to have
3specialist pathogens and predators. Field and herbarium surveys were thus used to determine if
4two pathogens (a smut and a rust) and a predispersal seed predator were less common at the
5western range limit of the forest sedge *Carex blanda* in Kansas, USA.
62. Host plant size, reproduction, and density did not decline at the western border of the range.
7In fact, plants at two western sites had unusually large size and seed production.
83. Host populations at the edge of the range were more likely to be disease-free or lack the
9predispersal seed predator. Where the smut, seed predator, and rust were found, the proportion
10of infected or infested plants was not related to longitude, latitude, or percent forest cover.
114. More of the peripheral populations lacked the smut than the rust, as expected given the more
12localised nature of smut spore dispersal and the limited period when smut infection can occur.
135. In the adjacent, more highly forested state of Missouri, there were no geographic patterns in
14the incidence of the smut or seed predator in herbarium data.
156. The smut and rust increased in frequency over the 129 year span of herbarium collections.
167. Although field and herbarium distributional data were not identical (for example, smut
17infection was found much farther west in the field than in the herbarium data), the qualitative
18agreement between the two datasets suggests herbarium data can be used more broadly for
19studies of natural enemy distributions.
208. Limited dispersal by pathogens and seed predators is probably the reason why small, isolated
21western populations were less likely to have natural enemies. Peripheral host populations may
22thus have different ecological and evolutionary trajectories compared to more central
23populations. This conclusion, as well as the considerable variation among peripheral

1populations, is relevant to geographical studies of coevolution and to research on climatic effects
2on plants inhabiting ecotonal regions.

3Key-words: *Anthracoidea blanda*, biogeography, central-marginal model, ecotone, host-

4pathogen interactions, peripheral populations, predispersal seed predator, *Puccinia*, smut, rust

1 Introduction

2 Research on the distributions of species, and their limits, is fundamental to the discipline of
3 ecology. Most distributional studies examine well-known taxa such as birds and plants, and
4 recently, marine invertebrates (Hengeveld & Haeck 1982; Brown 1984; Sagarin & Gaines
5 2002ab; Gaston 2003). Theoretical advances, however, have also emphasised the importance of
6 exploring distributions of parasites, pathogens, and mutualists (collectively, ‘natural enemies’)
7 and their hosts. With specialists, common sense and theory suggest that natural enemy
8 distributions will be constrained by host distributions, and will depend on colonisation and
9 extinction rates of the natural enemy and its host, as well as gradients in host habitat suitability
10 (Case *et al.* 2005). Hochberg & Ives (1999), extending Holt (1979), illustrated that parasitoids
11 with high dispersal rates may enforce host range limits. When dispersal is limited, however,
12 general metapopulation theory (Hanski & Ovaskainen 2000) suggests that isolated peripheral
13 host populations are likely to escape colonisation by specialist natural enemies. In such a
14 scenario, Antonovics *et al.* (2001) revealed that peripheral host populations could act as refugia,
15 and contribute to recolonisation of the center of the host range following an epidemic.

16 Documentation of host and natural enemy distributions at the borders of host ranges is an
17 essential first step in exploring the above theory. In the case of plants, it is known that
18 herbivorous insects often do not attack hosts across their entire range (Garcia *et al.* 2000, Brewer
19 & Gaston 2002). We do not know of explicit studies of plant disease in peripheral vs. more
20 central host populations. However, infection levels often vary spatially, and can be related to
21 environmental variables and/or the size and location of host populations (Kirby 1988; Burdon *et*
22 *al.* 1995; Ingvarsson & Ericson 1998; Ericson *et al.* 1999; Thrall *et al.* 2001; Smith *et al.* 2003;
23 Laine & Hanski 2006). Invasions of either hosts or pathogens/parasites also provide insight. For

1 example, peripheral chestnut populations remained free of the introduced chestnut blight fungus
2 for decades (Davelos & Jarosz 2004) and invasive plants may lose some of their pathogens as
3 they expand their range (Mitchell & Power 2003).

4 To address host/natural enemy distributions, we compared distributions of two pathogens
5 and one predispersal seed predator in peripheral vs. more central populations of the sedge *Carex*
6 *blanda*. *Carex blanda*, an understory plant, is found throughout the eastern forests of North
7 America, and reaches its western limits in the broad Great Plains ecotone where forests disappear
8 and grasslands predominate. Our work was focused in Kansas (KS), USA where precipitation
9 and percent forest cover both decrease from east to west. We explored three topics:

10 First, we examined the host plant, since variation in host suitability could influence natural
11 enemy distributions. We asked whether plant size and reproduction or plant density are reduced
12 as one reaches the range limits. A reduction in individual or population attributes would be
13 consistent with many studies (Hengeveld & Haeck 1982; Brown 1984; Carey *et al.* 1995;
14 Hochberg & Ives 1999; McGill & Collins 2003; Holt *et al.* 2005). However, exceptions also
15 exist, such as higher densities in the annual *Hornungia petraea* in peripheral populations (Kluth
16 & Bruelheide 2005), or Sagarin & Gaines' (2002ab) data on high densities of invertebrate
17 species near range edges. Other examples include work by Griggs 1914, Prince *et al.* 1985, and
18 Stokes *et al.* 2004.

19 Second, we explored geographic variation in levels of pathogen infection and seed
20 predation, and predicted that occurrence of these organisms would be reduced at the host range
21 limits for at least two reasons. One explanation focuses on the fact that western host populations
22 occur in a drier climate; precipitation and humidity often plays a key role in pathogen infection
23 (e.g. Huber & Gillepsie 1992). Another explanation, which is not mutually exclusive, is that

1western host populations are more isolated, which may reduce the probability of colonisation by
2pathogens or seed predators. Host population isolation is potentially captured by two geographic
3variables: longitude (western populations are further from the presumed eastern source
4populations of the natural enemies) and forest cover (western host populations often occur in
5small forest patches). Separating the independent roles of all three variables (precipitation,
6longitude, and forest cover) is challenging since they are intercorrelated. Focusing on two kinds
7of data on natural enemies may provide contrasts. For example, one might expect all three
8variables to lead to a lower likelihood of finding a pathogen or seed predator at a western
9location (i.e. presence/absence data). However, if one focuses on the percentage of plants
10infected/infested at only those locations where the natural enemy is found, we had different
11predictions for the precipitation vs. isolation variables. Specifically, if the progressively drier
12climate is of major importance, the percentage of plants infected/infested would be predicted to
13decrease as one moves westward. If limits on dispersal are crucial, western populations should
14often be free of pathogens and seed predators, but if a dispersal event does occur, the build-up of
15such populations at the site (and thus the observed percentage of infected or infested plants)
16could be unaffected by the site's isolation. Finally, we expect that natural enemies may differ in
17their distributions depending on their modes of dispersal and life histories.

18 The third goal of this study was methodological in nature. Ideally, biogeographic studies
19should focus on the entire species range (Sagarin & Gaines 2002a; Gaston 2003). However,
20such studies may only be feasible if ranges are small or linear (such as invertebrates along
21coastlines) (Sagarin & Gaines 2002b). Given these challenges, we were intrigued by Antonovics
22*et al.* (2003), which showed that herbarium specimens can provide distributional data on

1diseased plants. We compared KS distributional data from herbarium specimens to KS field data
2to evaluate if herbarium data can be used more broadly for studies of natural enemy distributions.

1Methods

2THE STUDY SYSTEM

3*Carex blanda* Dewey (Cyperaceae) is a common woodland sedge that occurs throughout the
4eastern deciduous forest in North America (Bryson 1980; Fig. 1). Plants are monoecious, flower
5in late April through to mid-May, and produce seeds from mid-May through to June. The plant
6lacks extensive clonal growth by rhizomes and thus occurs in discrete clumps.

7 We examined three natural enemies of *C. blanda*. The smut fungus *Anthracoidea blanda*
8(Vánky and H. Alexander) causes localised ovary infections (Vánky 2005). Individual infected
9flowers are sterilised with the ovaries replaced by sori that consist of fungal teliospores around
10remnant ovary tissue. An infected plant can range from having a single infected flower to over
1150% of flowers sterilised. Based on Scandianvian studies of other *Anthracoidea* species
12(Kukkonen 1972; Ericson *et al.* 1993; Ingvarsson & Ericson 1998, 2000), we expect that sori
13overwinter in the soil, teliospores germinate in the spring, and basidiospores infect developing
14flowers. Transmission of *Anthracoidea* is enhanced in Sweden by mycophagous beetles
15(Ericson *et al.* 1993); we have not observed these beetles in KS. Single seeds can also be killed
16by a seed predator. Infested seeds are greatly enlarged, and contain single white larvae which
17destroy the developing seed. These larvae were tentatively identified as chalcids (superfamily
18Chalcidoidea, order Hymenoptera; personal communications, J. Amrine); in this group, female
19wasps oviposit on developing seeds and the larvae feed and pupate in the seed. Usually < 5% of
20the seeds on a plant are affected. With the exception of very rare smut infection of *C. grisea*,
21smut and enlarged seeds were not observed on other co-occurring sedges.

22 The third natural enemy is a rust fungus in the *Puccinia caricina* species complex (based on
23ITS sequence comparisons with Gen Bank, L. Szabo, personal communications). Uredospores

1 are produced on leaves throughout the growing season, with teliospores appearing in the autumn.
2 In general, rusts reduce photosynthetic area (Lopes & Berger 2001), and thus plant growth.
3 Fifty six other *Carex* species are listed as hosts of *P. caricina* (Farr *et al.* 1989). However, the
4 four KS species on this list are aquatic and do not co-occur with *C. blanda* (C. Morse, personal
5 communications). The sexual stages of *P. caricina* occur on plants in the Urticaceae and
6 Grossulariaceae (Farr *et al.* 1989); plants in these families (e.g. *Ribes*, *Urtica*) have distributions
7 that span eastern – western KS (Great Plains Flora Association 1997) and were common at many
8 of our sites. However, since the rust identification occurred after the field work was completed,
9 we lack data on abundance of the alternate hosts at the sites, or infection levels.

10 FIELD SURVEYS

11 In May and early June of 2004 and 2005, we surveyed populations of *C. blanda* from eastern to
12 central KS. Twenty-six sites were surveyed in 2004; 31 sites (including all 2004 sites) were
13 surveyed in 2005 (see Table S1 in Supplementary Material, Fig. 1). We used linear transects
14 since the species often occurs along trails and streams. When *C. blanda* was first encountered at
15 a site, a continuous 30m transect was established, and the number of reproductive plants of *C.*
16 *blanda* was recorded for a 1m width on either side of the meter tape. Plants were scored for the
17 presence or absence of smut sori, enlarged seeds indicating predispersal seed predation, and rust
18 (only in 2005). Only flowering plants were recorded because sedge identification depends on
19 reproductive characters. Additional transects were established if the first transect had < 60
20 plants. In 2005, the 30m transect was subdivided into 15 2m x 1m segments, with counts made
21 in each segment to quantify plant density. We measured plant height (base to highest point of
22 plant) and basal diameter (using calipers) on three plants in 2004 and five plants in 2005; in
23 2005, we also measured the number of inflorescences, and for two inflorescences, the number of

1 seeds per inflorescence. Table S1 describes the 31 sites, their longitude and latitude using a
2 Global Positioning System (GPS) (Garmin GPSMAP 76, accuracy < 15m), their local habitat
3 (whether prone to flooding), and their understory vegetation cover as open (plants easily visible
4 on the forest floor), intermediate, or dense (plants hidden in dense vegetation).

5 We are confident that the central KS sites exist on the western range limit of *C. blanda*.
6 First, although no formal count was kept, we often explored over 10 woodland areas in central
7 KS before a single area with *C. blanda* was found; in eastern KS, the plant is found in virtually
8 every woodland. Second, our central KS locations are similar to the longitude of herbarium
9 specimens (Fig. 1). Finally, Kuchler (1974) delineated the pre-settlement western boundary of
10 where prairies had a significant amount of “islands” of forest vegetation; several central KS sites
11 are farther west than this boundary (Fig. 1).

12 For each site, we determined the average annual precipitation in mm (based on longterm
13 (typically 1948-2005) average annual rainfall data at the closest weather station, available
14 through the High Plains Regional Climate Center (www.hprcc.unl.edu/wrcc/states/ks.html), and
15 percent forest cover in a 200m radius circle around each site. The choice of the 200m distance
16 was arbitrary, but covered a wide range (near 0 – 100%) of forest cover (Table S1). Geographic
17 information system (GIS) work was done using Environmental Systems Research Institute’s
18 ArcGIS™, with supplementary work in MicroSoft Excel™. Percent forest cover was based on
19 KS land cover data from the US Geological Survey’s National Land Cover Dataset (NLCD)
20 (Vogelmann *et al.*, 1998). The NLCD is derived from Landsat satellite TM imagery from circa
21 1992. This dataset is in raster (Geo-TIFF) format, and is projected to Albers Conical Equal Area
22 North American Datum 1983; all spatial datasets were converted to this projection for analysis.
23 We used the Spatial Analyst extension to reclassify the 21 land cover classes into water, non-

1 forested, or forested areas, maintaining the original 30m resolution in the resulting grid dataset.
2 Forested areas included deciduous woods, evergreen woods, mixed woodlands, and woody
3 wetlands. We used geographic coordinates collected with a GPS to map sedge surveys from
4 2005, then generated a 200m radius circle around each site using the Buffer tool. To determine
5 percent forest cover within each site 'area', we performed a spatial cross tabulation between the
6 land cover data and the 200m radius circles, using the Tabulate Area tool.

7 HERBARIUM SURVEYS

8 A total of 1629 herbarium sheets were examined from KANU, R. L. McGregor Herbarium,
9 University of Kansas, Lawrence, KS; KSP, T. M. Sperry Herbarium, Pittsburg State University,
10 Pittsburg, KS; KSTC, Herbarium of Emporia State University, Emporia, KS; KSC, Herbarium,
11 Kansas State University, Manhattan, KS; MO, Herbarium at the Missouri Botanical Gardens, St.
12 Louis, MO; and MICH, Herbarium at University of Michigan, Ann Arbor, MI. These herbaria
13 are strong in central US and/or *Carex* collections. For each sheet we recorded the collector,
14 collection date, county and state, and presence vs. absence of smut sori or enlarged seeds
15 characteristic of the seed predator. We were not initially aware of the rust; we thus resurveyed
16 most KS sheets for presence/absence of rust (except those from the Herbarium at the Missouri
17 Botanical Gardens). All putative rust pustules were examined under a dissecting microscope.
18 Mycologists have been known to use herbaria as a source of fungal material. Although no such
19 annotations were evident, we asked herbarium directors whether there was any indication of
20 fungal removal over the history of their collections. All responses were negative.

21 We used herbarium data to provide presence/absence data by considering the specimen
22 (defined as all plants present on a sheet) infected or infested if any plants showed symptoms.
23 Further, since collectors sometimes distribute plants collected at a single location to multiple

1herbariums, we followed Antonovics *et al.* 2003 by defining all plants on multiple sheets that
2had the same collector, date, and location to be a single specimen. We limited analyses to KS or
3Missouri (MO) specimens; MO is a more heavily forested state in which *C. blanda* occurs
4throughout. Further, we restricted analyses to specimens for which we had complete location
5and date information, and for seasons where infection/infestation is detectable. We knew from
6field work that smut sori are not visible on infected inflorescences until late spring, and that in
7early and mid summer, respectively, predator-infested seeds and smut sori fall off the plant.
8Thus we limited our analyses of smut infection to specimens collected between May 12th – June
916th (KS: n = 116; MO: n = 327), and for seed infestation to collections prior to June 5th (KS: n
10= 183; MO: n = 414). These dates included the dates of the field surveys. We did not detect a
11significant seasonal effect on rust presence/absence, so the entire KS data set was used (n = 208).
12Finally, for all KANU specimens from KS, we recorded size data: height (cm; maximum height
13of plant) and inflorescence length (mm, average of two inflorescences). These variables were
14unlikely to be altered by the process of collecting or mounting a specimen; for example, basal
15diameter was not used because collectors often divide a large plant into smaller portions that fit
16on a herbarium sheet (C. Morse, personal communications).

17 Each herbarium specimen was assigned geographic coordinates (following Antonovics *et al.*
182003, these were based on the longitude and latitude of the county seat as not all records had
19specific location information), average annual precipitation (average of longterm data from all
20county weather stations; from the High Plains Regional Climate Center as noted earlier), and
21percent forest cover. To estimate forest cover by county, we obtained county boundary data for
22KS and MO in vector, ESRI shapefile format (U.S. Census Bureau, 2000). We performed a

1 spatial cross tabulation between the landcover and county datasets to obtain the percent forest
2 cover for each county.

3 ANALYSES

4 All statistical analyses were done in Minitab 14 (Minitab, Inc.) or SAS 9.1 (SAS Institute, Cary,
5 NC, USA). Initially, we analysed correlations between geographic variables for field sites and
6 counties (for herbarium data). Because of the very high correlation of KS longitude and
7 precipitation (see Results), we only included longitude in subsequent analyses.

8 *Analyses of Field Surveys*

9 Unless noted, analyses are for 2005, where we had more sites and more complete data (2004 and
10 2005 patterns were consistent - see correlation analyses in Results).

11 *Plant traits:* For individual plant traits and mean site density (number of plants in occupied 2m x
12 1m segments of the transects), we performed general linear models. Independent variables could
13 include survey date, geographic variables (longitude, latitude, forest cover), and local site
14 variables (habitat, cover, and population density). Plant size was calculated as plant basal area
15 (πr^2); this trait is highly correlated with biomass in plants with similar life forms to sedges (i.e.
16 grasses; Malmstrom *et al.* 2005). Plant size and mean seed production (number of
17 inflorescences x number of seed/inflorescence) were log-transformed to correct for heterogeneity
18 in variance. In these and similar analyses, full models with all predictor variables were run first,
19 and then nonsignificant terms were eliminated in subsequent model runs. Habitat and cover
20 variables were only eliminated if their interaction was not significant. Type III sums of squares
21 were used so that the order variables entered in the model did not alter the results.

22 *Pathogen and seed predator levels:* We analysed natural enemy distributions in three ways.
23 First, the presence/absence of disease and predation at the sites were examined with logistic

1 regression. Second, we took a community approach by scoring each site as having 0, 1, 2, or 3
2 pathogen or predator species present and analysing the data using ordinal logistic regression.
3 Finally, for sites where a particular pathogen or predator was present, we analysed variation in
4 the percentage of plants with infection or predation with general linear models on arcsine-
5 transformed data. The independent variables were the same as described above for analyses of
6 plant traits. In logistic regressions, the vegetation cover variable had to be deleted so that
7 algorithms would converge. We present two tests used in Minitab 14 to describe logistic
8 regressions: a Z test of whether each coefficient for a model predictor was significantly different
9 from zero, and a G statistic which tests whether all slopes are equal to zero.

10 *Analyses of herbarium surveys*

11 *Coverage:* To examine the geographic coverage of collections, we used resampling methods
12 for each state for the entire plant collection, as well as specimens with each natural enemy.
13 Following Antonovics *et al.* (2003), a specimen was randomly sampled without replacement and
14 the county name was noted. This process was repeated for the entire collection, noting whether
15 subsequent specimens provided new county names. The collection of specimens was then
16 randomised, and the process was repeated 100 times. In coverage curves, the x axis is the
17 position of the specimen in the collection (i.e. first, second,...last examined) and the y axis is the
18 proportion of the 1000 randomisations that resulted in a new county at that position.

19 *Plant traits:* Using general linear models, we explored whether plant height or average
20 inflorescence length was predicted by collection date, longitude, latitude, or forest cover.

21 *Pathogen and seed predator levels:* We performed multivariate logistic regression on the
22 presence/absence of each natural enemy, with the initial full model using the collection year and
23 geographic variables (see *Analyses of Field Surveys* for details). Analyses were done by state

1 and for a combined data set. To present relationships from these logistic regressions, we divided
2 each data set using the median value of the independent variable, and calculated the percentage
3 of infected/infested individuals in each data set half. The equal sample sizes of the two halves of
4 the data set circumvents issues of whether infection/infestation rates are rare in western
5 specimens because fewer were collected at the range limit. In parallel with community analyses
6 of field data, we used an ordinal logistic regression to analyse whether 0, 1, 2, or all 3 of the
7 natural enemies were detected in each KS county. The number of specimens per county was
8 included in analyses to account for variation in sampling intensity among counties.

9 In addition to using collection year in the above logistic regressions, we also explored
10 temporal trends by calculating the percent of infected or infested specimens in three time
11 intervals (≤ 1920 , 1920-1960, > 1960). Although our specimens ranged from 1874 to 2003,
12 specimen numbers per decade varied greatly. We chose these three intervals to have sufficient
13 sample sizes per interval and to allow comparisons among the three natural enemies.

1 Results

2 WHAT ARE THE RELATIONSHIPS BETWEEN GEOGRAPHIC VARIABLES?

3 As expected, KS locations with more western longitudes had lower precipitation ($r = -0.97$, $p <$
4 0.0001 ; $r = -0.93$, $p < 0.0001$, statistics for sites and counties, respectively) and lower forest
5 cover ($r = -0.70$, $p < 0.0001$; $r = 0.79$, $p < 0.0001$), while locations with higher precipitation had
6 higher forest cover ($r = 0.62$, $p < 0.0001$; $r = 0.71$, $p < 0.0001$). The latitude of a location was
7 not significantly correlated with other variables in the field data; in the herbarium data, southern
8 counties had higher precipitation ($r = -0.37$, $p < 0.01$). Because KS longitude and precipitation
9 were so strongly correlated, we only included longitude in KS analyses. Similar, although
10 weaker, correlations occurred in the MO herbarium data (precipitation and longitude, $r = -0.58$, p
11 < 0.0001 ; precipitation and forest cover, $r = 0.42$, $p < 0.0001$, longitude and forest cover $r = -0.49$
12, $p < 0.0001$); in addition, southern counties had higher forest cover ($r = 0.48$, $p < 0.0001$).

13 IS PLANT SIZE OR DENSITY REDUCED AT THE RANGE LIMIT?

14 *KS field surveys*

15 Despite considerable variation, average plant size increased to the west ($F_{1,28} = 6.8$, $p = 0.01$) and
16 at sites with lower forest cover ($F_{1,28} = 6.2$, $p = 0.02$) ($R^2 = 0.21$). Average seed number per plant
17 increased to the west also ($F_{1,29} = 6.73$, $p < 0.01$, $R^2 = 0.19$) (Fig. 2). Two peripheral host
18 populations with unusually large plants greatly affected the relationships (Fig. 2). If these two
19 populations were removed from the analyses, plant size increased with population latitude ($F_{1,27}$
20 $= 4.4$, $p = 0.05$, $R^2 = 0.14$) and no factor predicted seed number per plant. Plant density did not
21 vary geographically but highest densities were found in lowland habitats with open cover (Fig.
22 23). For the 18 sites examined at comparable census dates, 2004 plant size was positively
23 correlated with 2005 plant size ($r = 0.6$, $p = 0.02$).

1 *KS herbarium surveys*

2 Plant height and inflorescence length of herbarium specimens did not vary with latitude,

3 longitude, or forest cover.

4 AT THE RANGE LIMIT, IS IT MORE LIKELY THAT SITES WILL LACK DISEASE OR

5 SEED PREDATION?

6 *KS field surveys*

7 The 31 sites varied greatly in smut, seed predator, and rust levels (Table S1); such differences
8 appear to be characteristic of the sites given positive correlations between percentage of plants
9 with smut infection ($r = 0.75$, $p < 0.0001$) and with seed predation ($r = 0.69$, $p < 0.001$) for sites
10 visited in the same two weeks in 2004 and 2005. The percentage of plants with smut or seed
11 predators was correlated across all sites ($r = 0.36$, $p = 0.04$), but we found no significant
12 correlation between these organisms when examining the 22 sites that had both organisms. Rust
13 infection was not significantly correlated with either the smut or seed predator. Lack of strong
14 correlations between species led us to analyse each natural enemy separately.

15 The nine smut-free sites were all located at the western margin, particularly in the south
16 (Table S1, Fig. 1), leading to significant longitude ($Z = 2.17$, $p = 0.03$) and latitude ($Z = 2.23$, $p =$
17 0.03) effects in logistic regression (for the model, $G = 18.978$, d. f = 1, $p < 0.001$). The three
18 seed predator-free and two rust-free sites were also located on the range limit. Due to the small
19 sample sizes, the effect of longitude was only marginally significant for the seed predator data
20 set ($Z = 1.84$, $p = 0.07$), and the logistic regression algorithm did not converge for the rust data.

21 From a community perspective, the number of natural enemy species/site was reduced at the
22 range limit (Table S1; Fig. 4a), leading to significant coefficients for longitude ($Z = 2.24$, $p =$

10.03) and latitude ($Z = -2.91$, $p < 0.01$) in multivariate logistic regression (test that all slopes were 0 in the model: $G = 25.273$, $p < 0.001$, d.f. = 2).

3Herbarium surveys

4*Carex blanda* occurred in 52 KS counties, with eight, 15, and 48 counties having specimens with 5smut, seed predators, or rust, respectively (Fig. 1). In MO, 95 of the 114 counties had *C.*

6*blanda*; the smut and seed predator were found in 14 and 32 counties, respectively. The

7geographic coverage for the plant and rust in KS was excellent (Fig. 5ad). Despite the small

8number of smutted specimens, smut coverage was fair, with the probability of adding another

9county to the distribution reduced to 0.26 when all specimens had been examined (Fig. 5c).

10Coverage was spottier for the seed predator with final probabilities of adding new counties to the

11distribution near 0.5 (Fig.5b). MO plant coverage was very similar to KS; coverage for MO

12smut and seed predator data appears similar to the KS seed predator data.

13 The presence/absence of one pathogen or predator species on a specimen was statistically

14independent of the presence/absence of other species (contingency tests; in all cases, $p \geq 0.1$).

15For KS, 10.3% of the specimens had smut, 10.4% had seed predators, and 75.3% had rust. Smut

16was more likely to be absent on western KS specimens; the exact significance of this result from

17the multivariate logistic regression depends on the statistical test (Z test for whether coefficient

18was different from 0 = -1.77, $p < 0.08$; G test that all slopes are 0 is $G = 5.55$, d.f. = 1, $p = 0.02$).

19The likelihood of detecting the seed predator was lower for specimens collected in counties with

20lower forest cover ($Z = 2.20$, $p = 0.03$, $G = 5.184$, d.f. = 1, $p = 0.02$). Rust was less likely to be

21observed in western KS specimens ($Z = 2.04$, $p = 0.04$) and has become more common in recent

22years ($Z = 2.85$, $p < 0.01$) (final model, $G = 12.526$, d.f. = 2, $p < 0.01$). These spatial and

23temporal relationships are illustrated in Table 1. In the community analysis, species number

1declined as forest cover declined (Fig. 4b, $Z = -2.88$, $p < 0.01$). As expected, we detected more
2natural enemy species for counties with more specimens ($Z = -1.94$, $p = 0.05$); for the final
3model, $G = 31.872$, d.f. = 2, $p < 0.001$).

4 The percentage of MO specimens with smut (5.5 %) and seed predators (10.4%) was
5generally similar to KS. The geographic variables didn't explain the presence/absence of the
6smut or seed predator in MO or in the combined state dataset; however, there was an increase in
7smut infection over time (for combined dataset: $Z = 2.02$, $p = 0.04$; $G = 5.373$, d.f. = 1, $p = 0.02$)
8(Table 1).

9WAS THERE A LOWER PERCENTAGE OF PLANTS WITH NATURAL ENEMIES AT
10THE RANGE LIMIT?

11We found no geographic pattern to the percentage of plants infected or infested when we
12restricted analyses to only sites where the pathogen or seed predator was present. In fact, several
13western sites had high percentages of plants with disease or seed predation (Table S1).

14

15

16

17

18

19

20

21

22

1Discussion

2INDIVIDUAL AND POPULATION LEVEL TRAITS OF PLANTS ACROSS THE EAST- 3WEST GRADIENT

4We found no evidence for reduced plant size, reproduction, or density at the western range limit.
5In fact, the largest plants and some of the highest densities occurred at two far western sites,
6emphasising the value of intensive sampling at a species' limits (Sagarin & Gaines 2002a).
7These two western sites were not obviously different from other sites. Since data were only
8taken on flowering plants, one might hypothesise that only the largest plants flowered in the west
9while a wider range of plant sizes flowered in the east. However, no such patterns in flowering
10were observed. The reduced incidence of the natural enemies we studied also does not explain
11plant patterns. The smut and seed predator are limited to individual flowers and shouldn't affect
12plant growth. Rust can reduce plant growth, but some western sites had high rust levels and very
13large plants (site 29, Table S1). Other unmeasured variables may have been important. For
14instance, trees were sparse at some western sites, allowing greater light to the understory. The
15absence of pathogens we did not study (e.g. soil-borne organisms, viruses) might also have been
16important. Regardless of mechanism, we show that range limits *per se* are not always associated
17with reduction in plant performance, as also found by Stokes *et al.* (2004) and Kluth &
18Bruehlheide (2005). Our results further argue against a westward decline in host suitability for
19natural enemies; in fact, the larger size and reproduction in some western sites suggest greater
20host suitability.

21PATHOGEN INFECTION AND SEED PREDATION ACROSS THE EAST-WEST 22GRADIENT

1 We found few factors that predict pathogen or predator levels at the local site level; we thus
2 focus on larger spatial scale patterns. All three natural enemies did have widespread
3 distributions (Fig. 1, Table S1). However, if one examines the presence or absence of a pathogen
4 or seed predator at locations, there was a lower probability of finding these three organisms on
5 the western host limit. If one focuses only on sites where the natural enemy was present, we did
6 not discern any geographic patterns to the percentage of plants infected or infested. This latter
7 result suggests that host populations across KS are largely suitable for these natural enemies, and
8 argues against the general westward decline in precipitation as the primary determinant of
9 pathogen and predator distributions. For example, fungal infection can probably occur in the
10 drier western climate because of higher humidity in microclimates in woods and along creeks,
11 where *C. blanda* is often found. Low probability of dispersal to isolated western populations
12 thus probably explains the absence of the smut, and to a less degree, the rust and the seed
13 predator, at the range limit. This conclusion is consistent with the lack of geographic patterns in
14 smut or seed predator incidence in MO, where forest cover is higher (average % forest cover per
15 county = 38%) and understory forest species are likely to have more continuous distributions.
16 Our interpretations of cause and effect at the state-wide level must be tempered by the very high
17 correlation between geographical variables, especially between longitude and precipitation. In
18 our analyses, we also note that we treated field sites as independent data points. We made this
19 decision because even sites separated by short distances could have very different frequencies of
20 natural enemies (Table S1). However, as one goes from MO to central KS, forest fragmentation
21 changes from a patchy landscape to linear forest fragments along creeks and rivers. Possible
22 long-distance dispersal of pathogens or seed predators between connected forest fragments
23 deserves further study.

1 Dispersal mechanisms and life histories differ among pathogen species, with important
2 ecological and genetic consequences (Thrall & Burdon 1999). For example, in contrast to the
3 smut and seed predator, the distribution of alternate hosts may have major effects on the
4 distribution of *P. caricina*. We lack data to explore such patterns, but as noted in the Methods,
5 data from plant atlases suggest that sexual and asexual hosts of the rust co-occur across Kansas.
6 We did find that the smut had a more restricted KS distribution than the rust, especially in the
7 field data. This result may be explained by different modes of spore dispersal. For instance,
8 teliospores from smutted inflorescences overwinter at the base of plants; the following spring,
9 basidiospores disperse by very local air movement. In contrast, rust urediospores can disperse in
10 the atmosphere over 100 km (Eversmeyer & Kramer 2000). Susceptible tissues are also present
11 on the host for a shorter time for the smut (immature flowers present for 2-3 weeks) vs. the rust
12 (leaf tissue present for months). The limited spore dispersal of the smut, and its absence in
13 several western sites, could be considered in relation to theoretical work by Bahn et al. (2006),
14 who showed that unsuccessful dispersal from isolated peripheral populations can contribute to
15 extinctions and the formation of range limits. However, although smut did disappear at one
16 transect between 2004 and 2005 near the host range limits (site 14, Table S1), transect data on
17 extinctions are inconclusive since these organisms may exist elsewhere in the forest patch.

18 Smut and seed predation levels in 2004 and 2005 were strongly correlated across the sites.
19 Positive year-to-year correlations were also apparent for similar organisms in Sweden at a
20 smaller spatial scale (infection/infestation of tussocks by a congeneric smut, *A. heterospora* and
21 a mite *Phytoptus caricis*, Ingvarsson & Ericson 1998). These Swedish flower-inhabiting species
22 compete for shared ovary resources, especially when present at high densities (Ingvarsson &
23 Ericson 2000). We found that the levels and distributions of the smut and seed predator of *C.*

1 *blanda* were largely independent of each other. Ovary resources may not have been limiting
2 since plants were not completely smutted or infested with seed predators, even when the
3 percentage of infected/infested plants was high.

4 USE OF FIELD AND HERBARIUM DATA TO STUDY PATHOGEN AND PREDATOR 5 DISTRIBUTIONS

6 Recent investigations (Antonovics *et al.* 2003 (and references within); Hood & Antonovics
7 2003) have used herbaria to study plant-pathogen interactions. Our work is unusual in that we
8 compare data from herbarium and field surveys. Both field and herbarium approaches have pros
9 and cons. In the field, a researcher can examine many plants/site and collect detailed data at
10 each site. However, finding sites and recording data is time-consuming and reduces the number
11 of total sites examined; this was challenging given the narrow temporal window when smut
12 infection and seed predation could be scored. In particular, we are aware that although we did
13 intensive field sampling in the west, we had fewer field sites in eastern KS simply because of the
14 difficulty in visiting many sites within the appropriate timeframe. We doubt if more sampling
15 would alter our overall conclusions (although since our study was completed, we have identified
16 some eastern sites that may be smut-free). In the future, we would like to focus on one
17 latitudinal region and intensively sample sites to determine if correlations between site isolation
18 and smut infection occur.

19 In contrast to field sampling, surveys of herbarium collections allow one to examine plants
20 from hundreds of locations. However, bias can be introduced depending on where collectors go
21 and which plants they collect. Some biases can be addressed in a qualitative manner by
22 comparing field and herbarium datasets. For example, rust was common in both datasets.
23 Higher rust incidence in the herbarium dataset may reflect the fact that plants were examined

1microscopically; hence even single pustules were detected. Bias may exist against collecting
2smutted plants: smut infection was similar (KS) or smaller (MO) than seed predation in the
3herbarium data set, but was at a similar level or more common at most field sites (Table S1).
4Further, heavily smutted plants were less common in the herbarium data than in the field.
5However, importantly, such biases should not lead to geographic patterns; for example, it is not
6obvious that western collectors would be more likely to avoid smutted plants than eastern
7collectors. Another challenge of herbarium data, incomplete coverage, can be quantified due to
8approaches such as Antonovics *et al.* 2003. Such resampling methods look at patterns in the
9actual data: incomplete coverage due to collectors never working in parts of a species' range will
10obviously not be detected. We were pleased by how generally high the coverage was, given the
11limited number of specimens, although distributional data on the smut and seed predator is far
12from complete.

13 Herbarium and field surveys also differ in spatial and temporal scales. From a
14methodological perspective, we knew the exact longitude and latitude of a field site, and thus
15investigated whether fine-scale forest cover (200m radius circle) was a predictor in analyses.
16Such fine-scale analyses were impossible for the herbarium specimens, where precise location
17data were often missing. Thus, we analysed the herbarium data at the spatial scale of a county,
18where, due to greater coverage across the state, we could look for larger scale spatial patterns.
19Field surveys also provide an instantaneous “snapshot” of distributions in contrast to the
20cumulative distributions resulting from multiyear herbarium surveys. Antonovics *et al.* (2001)
21noted chance dispersal events or short-lived persistence of populations at the far margins of a
22species' range may be sampled by collectors. Thus a cumulative collection may imply a broader
23range distribution than is typically seen in any single year. In contrast, however, the western

1 boundary for *C. blanda* in our herbarium and field data were similar, and field surveys extended
2 the western limit of the smut and seed predator (but not the rust) (Fig. 1). The narrower spatial
3 distribution of the smut and seed predator in the herbarium vs. the field survey probably reflects
4 sampling intensity. A herbarium sheet has only 1–5 plants; thus even without any bias against
5 plants with disease or predation, the probability of detection of natural enemies at any single site
6 using a herbarium collection is low. Further, the number of herbarium specimens per county
7 declined as one moved from east to west in KS. In contrast, we purposely did intensive field
8 sampling at the western range limit and thus by sampling many populations and plants, were
9 more likely to detect the smut and seed predator. Because of differences between approaches,
10 we did not expect that herbarium distributions of natural enemies would match distributions
11 uncovered in field surveys. However, as emphasised by Antonovics *et al.* (2003), *relative*
12 comparisons are valuable. Hence we find it encouraging that the western vs. eastern differences
13 in presence/absence of disease and seed predation occurred in both data sets. The somewhat
14 lower percentage of smutted specimens in MO than KS (5.5% compared to 10.3%) was
15 surprising, but given the difference was not significant, it may be due to chance sampling.

16 An unexpected result was that the percentage of specimens with smut and rust increased
17 significantly over the >100 year span of herbarium collections, and a similar trend was found for
18 seed predation. As noted in the Methods, we lack evidence that herbarium specimens were
19 “mined” by early mycologists. It is also doubtful that any biases against collecting infected
20 material would change across time. However large changes in the landscape and land use
21 occurred over the 129 year span of the collections. By comparing modern forest cover to
22 historical records (Fifth Annual Report of the State Board of Agriculture 1877), we found that
23 there was no net change in forest cover west of 96° W longitude, where peripheral host

1populations are located. However, 5-10% of eastern KS was forested in the late 1800's, while
2current estimates are 10-20% (Fig. 1). Disease levels possibly have increased in parallel with the
3increase in forest cover since increased forest cover is likely to be associated with increased
4abundance and reduced isolation of populations of *C. blanda*. Grazing pressures or frequencies
5of the alternate hosts of the rust may also have changed over time. Interestingly, Antonovics *et*
6*al.* (2003) reported a 16% increase in smut infection in *Silene* over a 100 year span of herbarium
7collection and Bearchell *et al.* (2005) inferred that the relative abundance of two wheat
8pathogens in dried plant material has changed over a 160 year span. The changes in the wheat
9pathogen population dynamics were correlated with changes in atmospheric pollution.

1Conclusion

2 We found no evidence of reduced size, reproduction, or density at range limits and
3 discovered surprisingly large plants with high seed production at some western sites. Smut, seed
4 predators, and rust were commonly found in much of the host range in KS, but were more likely
5 to be absent in peripheral host populations, probably due to limits on dispersal. In the future,
6 distributional studies need to be paired with analysis of host resistance and pathogen virulence
7 structure. Such work could be particularly informative in light of coevolutionary theory
8 (Nuismer *et al.* 2003; Thompson 2005) and since peripheral plant populations can have restricted
9 genetic variation (Lesica & Allendorf 1995). We expect that ecological and genetic studies of
10 peripheral populations will become of increasing interest; borders of species' distributions
11 (Parmesan & Yohe 2003) and disease (Harvell *et al.* 2002) are predicted to change as a result of
12 global phenomenon and such changes may be more evident at ecotones (Neilson 1993).

13Acknowledgments

14 We appreciate those who assisted with surveys (J. Emry, M. Forester, F. Price, D. Schroeder, A.
15 ShabShab), species identification (J. Amrine, C. Freeman, C. Morse, J. O'Mara, Y. Ono, M.
16 Palm, L. Szabo, K. Vánky), and comments on the manuscript (J. Antonovics, R. Holt, C.
17 Malmstrom, J. Moody-Weis, E. Tarr, and an anonymous reviewer). C. Collins created the
18 figures. The University of Kansas Field Station and Ecological Reserves, the Konza Prairie
19 Biological Station, J. Elliot, M. Maier, and the ShabShab family provided access to field sites.
20 C. Morse and C. Freeman made the R. L McGregor Herbarium available to us and arranged for
21 all herbarium loans. Funding included a National Science Foundation grant (NSF DEB0128810
22 to H.M.A, including a REU supplement for S. P.), a University of Kansas General Research

1Fund Grant (2301547-003), and an Educational Opportunity Award from the University of
2Kansas Student Senate for S.P.

1References

- 2Antonovics, J. A., Newman, T. J., & Best, B. J. (2001) Spatially explicit studies on the ecology
3 and genetics of population margins. *Integrating Ecology and Evolution in a Spatial Context*
4 (eds J. Silvertown and J. Antonovics), pp 97-116. Blackwell Science, Oxford.
- 5Antonovics, J., Hood, M. E., Thrall, P. H., Abrams, J. Y., & Duthie, G. M. (2003) Herbarium
6 studies on the distribution of anther-smut fungus (*Microbotryum violaceum*) and *Silene*
7 species (Caryophyllaceae) in the eastern United States. *American Journal of Botany*, **90**,
8 1522-1531.
- 9Bahn, V., O'Connor, R. J., & Krohn, W. B. (2006) Effect of dispersal at range edges on the
10 structure of species ranges. *Oikos* (in press).
- 11Bearchell, S. J., Fraaije, B. A., Shaw, M. W., & Fitt, B. D. L. (2005). Wheat archive links long-
12 term fungal pathogen population dynamics to air pollution. *Proceedings of the Natural*
13 *Academy of Sciences*, **102**, 5438-5442.
- 14Brewer, A. M. and Gaston, K. J. (2002). The geographic range structure of the holly leaf-miner.
15 I. Population density. *Journal of Animal Ecology*, **71**, 99-111.
- 16Brown, J. H. (1984) On the relationship between abundance and distribution of species.
17 *American Naturalist*, **124**, 255-279.
- 18Bryson, C. T. (1980) *A Revision of the North American Carex Section Laxiflorae (Cyperaceae)*.
19 Dissertation. Mississippi State University.
- 20Burdon, J. J., Ericson, L., & Muller, W. J. (1995) Temporal and spatial changes in a
21 metapopulation of the rust pathogen *Triphragmium ulmariae* and its host, *Filipendula*
22 *ulmaria*. *Journal of Ecology*, **83**, 979-989.

1 Carey, P. D., Watkinson, A. R., & Gerard, F. F. O. (1995) The determinants of the distribution
2 and abundance in the winter annual grass *Vulpia ciliata* ssp. *Ambigua*. *Journal of Ecology*,
3 **83**, 177-187.

4 Case, T. J., Holt, R. D., McPeck, M. A., & Keitt, T. H. (2005) The community context of
5 species' borders: ecological and evolutionary perspectives. *Oikos*, **108**, 28-46.

6 Davelos, A. L. & Jarosz, A. M. (2004) Demography of American chestnut populations: effects of
7 a pathogen and a hyperparasite. *Journal of Ecology*, **92**, 675-685.

8 Ericson, L., Burdon, J. J. & Wennström, A. (1993) Inter-specific host hybrids and phalacrid
9 beetles implicated in the local survival of host pathogens. *Oikos*, **68**, 393-400.

10 Ericson, L., Burdon, J. J., & Müller, W. J. (1999) Spatial and temporal dynamics of the rust
11 fungus *Uromyces valerianae* on populations of its host *Valeriana salina*. *Journal of*
12 *Ecology*, **87**, 649-658

13 Eversmeyer, M. G. & Kramer, C. L. (2000) Epidemiology of wheat leaf and stem rust in the
14 Central Great Plains of the USA. *Annual Review of Phytopathology*, **38**, 491-503.

15 Farr, D. F., Bills, G. F., Chamuris, G. P., & Rossman, A. Y. (1989). *Fungi on Plants and Plant*
16 *Products in the United States*. APS Press. St. Paul, MN

17 Fifth Annual Report of the State Board of Agriculture (1877) Geo. W. Martin, Kansas
18 Publishing House.

19 García, D., Zamora, R., Gómez, J. M., Jordano, P., & Hódar, J. (2000) Geographic variation in
20 seed production, predation and abortion in *Juniperus communis* throughout its range in
21 Europe. *Journal of Ecology*, **88**, 436-446.

22 Gaston, K. J. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University
23 Press. Oxford.

- 1 Great Plains Flora Association. (1997) *Atlas of the Flora of the Great Plains*. Iowa State
2 University Press. Ames, Iowa.
- 3 Griggs, R. F. (1914) Observations on the behavior of some species at the edges of their ranges.
4 *Bulletin of the Torrey Botanical Club*, **41**, 25-49.
- 5 Hanski, I & Ovaskainen, O. (2000). The metapopulation capacity of a fragmented landscape.
6 *Nature* 404:755-758.
- 7 Harvell, C. D., Mitchell, C. E., Ward, J. R., Altizer, S., Dobson, A. P., Ostfeld, R. S., and
8 Samuel, M. D. (2002) Climate warming and disease risks for terrestrial and marine biota.
9 *Science* 296: 2158-2162.
- 10 Hengeveld, R. & Haeck, J. (1982) The distribution of abundance. I. Measurements. *Journal of*
11 *Biogeography*, **9**, 303-316.
- 12 Hochberg, M. E. & Ives, A. R. (1999) Can natural enemies enforce geographic range limits?
13 *Ecography*, **22**, 268-276.
- 14 Holt, R. D. 1979. Predation and the structure of prey communities. Ph.D. Thesis. Harvard
15 University.
- 16 Holt, R. D., Keitt, T. H., Lewis, M. A., Maurer, B. A., & Taper, M. L. (2005). Theoretical
17 models of species' borders. *Oikos*, **108**, 18-27.
- 18 Hood, M. E. & Antonovics, J. (2003) Plant species distributions show signs of disease.
19 *Proceedings of the Royal Society Biological Sciences Series B*, **270 (Supplement 2)**, S156-
20 S258.
- 21 Huber, L. & Gillespie, T. J. (1992) Modeling leaf wetness in relation to plant disease
22 epidemiology. *Annual Review of Phytopathology*, **30**, 553-577.

1 Ingvarsson, P. K. & Ericson, L. (1998) Spatial and temporal variation in disease levels of a
2 floral smut (*Anthracoidea heterospora*) on *Carex nigra*. *Journal of Ecology*, **86**, 53-61.

3 Ingvarsson, P. K. & Ericson, L. (2000) Exploitative competition between two seed parasites on
4 the common sedge, *Carex nigra*. *Oikos*, **91**, 362-370.

5 Kirby, G. C. (1988) The population biology of a smut fungus, *Ustilago spinificis* Ludw. I.
6 Geographic distribution and abundance. *Australian Journal of Botany*, **36**, 339-346.

7 Kùchler, A. W. (1974) A new vegetation map of Kansas. *Ecology*, **55**, 586-604.

8 Kukkonen, I. (1972) Micro- and macro-ecological factors in the speciation of obligate parasites.
9 *Annals of Botany*, **36**, 1029-1040.

10 Kluth, C. & Bruelheide, H. (2005). Central and peripheral *Hornungia petraea* populations:
11 patterns and dynamics. *Journal of Ecology*, **93**, 584-595.

12 Laine, A. & Hanski, I. (2006) Large-scale spatial dynamics of a specialist plant pathogen in a
13 fragmented landscape. *Journal of Ecology*, **94**, 217-226.

14 Lesica, P. & Allendorf, F. W. (1995) When are peripheral populations valuable for
15 conservation? *Conservation Biology*, **9**, 753-760.

16 Lopes, D. B. & Berger, R. D. (2001) The effects of rust and anthracnose on the photosynthetic
17 competence of diseased bean leaves. *Phytopathology*, **91**, 212-220.

18 Malmstrom, C. M, Hughes, C. C, Newton, L. A., & Stoner, C. J. (2005) Virus infection in
19 remnant native bunchgrasses from invaded California grasslands. *New Phytologist*, **168**,
20 217-230.

21 McGill, B. & Collins, C. (2003) A unified theory for macroecology based on spatial patterns of
22 abundance. *Evolutionary Ecology Research*, **5**, 469-492.

1 Mitchell, C. E. & Power, A. G. (2003) Release of invasive plants from fungal and viral
2 pathogens. *Nature*, **421**, 625-627.

3 Neilson, R. P. (1993) Transient ecotone response to climatic change: some conceptual and
4 modelling approaches. *Ecological Applications*, **3**, 385-395.

5 Nuismer, S. L., Thompson, J. N., & Gomulkiwicz, R. (2003). Coevolution between hosts and
6 parasites with partially overlapping geographic ranges. *Journal of Evolutionary Biology*, **16**,
7 1337-1345.

8 Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts
9 across natural systems. *Nature*, **421**, 37-42.

10 Prince, S. D., Carter, R. N., & Dandcy, K. J. (1985) The geographic distribution of prickly
11 lettuce (*Lactuca serriola*). II. Characteristics of populations near its distribution limit in
12 Britain. *Journal of Ecology*, **73**, 39-48.

13 Sagarin, R. D. & Gaines, S. D. (2002a) The 'abundant centre' distribution: to what extent is it a
14 biogeographical rule? *Ecology Letters*, **5**, 137-147.

15 Sagarin, R. D. & Gaines, S. D. (2002b) Geographic abundance distributions of coastal
16 invertebrates: using one-dimensional ranges to test biogeographic hypotheses. *Journal of*
17 *Biogeography*, **29**, 985-997.

18 Smith, D. L., Ericson, L., and Burdon, J. J. (2003) Epidemiological patterns at multiple spatial
19 scales: an 11-year study of a *Triphragmium ulmariae-Filipendula ulmaria* metapopulation.
20 *Journal of Ecology*, **91**, 890-903.

21 Stokes, K. E., Bullock, J. M., & Watkinson, A. R. (2004) Population dynamics across a
22 parapatric range boundary: *Ulex gallii* and *Ulex minor*. *Journal of Ecology*, **92**, 142-155.

- 1Thompson, J. N. (2005) *The Geographic Mosaic of Coevolution*. University of Chicago Press.
2 Chicago.
- 3Thrall, P. H. & Burdon, J. J. (1999) The spatial scale of pathogen dispersal: consequences for
4 disease dynamics and persistence. *Evolutionary Ecology Research*, **1**,681-701.
- 5Thrall, P. H., Burdon, J. J., & Bock, C. H. (2001) Short-term dynamics in the *Cakile maritima*-
6 *Alternaria brassicicola* host-pathogen association. *Journal of Ecology*, **89**, 723-735.
- 7U.S. Census Bureau. 2000. Topologic Integrated Geographic Encoding and Referencing
8 (TIGER) files. http://www.census.gov/geo/www/cob/bdy_files.html.
- 9Vánky, K. (2005). Taxonomic studies on Ustilaginomycetes – 25. *Mycotaxon*, **91**, 217-272.
- 10Vogelmann, J. E., Sohl, T. L., Campbell, P. V., & Shaw, D. M. (1998) Regional land cover
11 characterization using Landsat Thematic Mapper data and ancillary data sources.
12 *Environmental Monitoring and Assessment*, **51**, 415-428.

1 Table 1. Spatial and temporal variation in disease and seed predation based on herbarium specimens. A Spatial variation in
 2 percentage of specimens with smut, seed predation, and rust in KS for variables that were significant in multivariate logistic regression
 3 (see text). The percentage infected or infested was calculated for western vs. eastern longitudes, or lower vs. higher values of percent
 4 forest cover by using the median value of the predictor variable to divide the data set in half. B. Temporal variation in percentage of
 5 specimens with smut, seed predation, and rust. Data were divided in 40 year intervals using the combined KS and MO datasets (for
 6 smut and seed predator) or the KS data (for rust). Significant temporal variation was found for smut and rust in multivariate logistic
 7 regression (see text); For both A. and B., samples sizes are indicated in parentheses; p values listed in tables are based on Chisquare
 8 or Fisher¹ exact tests.

9 A. Spatial variation

	Longitude		
	Western	Eastern	
10			
11			
12% with smut	3.4 (n = 58)	17.2 (n = 58)	$\chi^2 = 4.949, d.f. = 1, p = 0.015$
13% with rust	68.6 (n=99)	81.8 (n = 99)	$\chi^2 = 4.583, d.f. = 1, p = 0.032$
14			
	% Forest Cover		
	Low	High	
15			
16% with seed predation	4.4 (n = 91)	16.3 (n = 92)	$\chi^2 = 6.973, d.f. = 1, p = 0.008$
17			

1

2B. Temporal variation

3

% of plants with

4

Smut

Seed predator

Rust

5 Before or equal to 1920

0 (n = 56)

4.0 (n = 76)

52.2 (n = 23)

6 1921-1960

1.8 (n = 55)

12.2 (n = 90)

64.7 (n = 34)

7 After 1960

8.7 (n = 332)

11.1 (n = 431)

80.1 (n = 151)

8

$p^1 = 0.009$

$\chi^2 = 3.9, \text{d.f.} = 2$

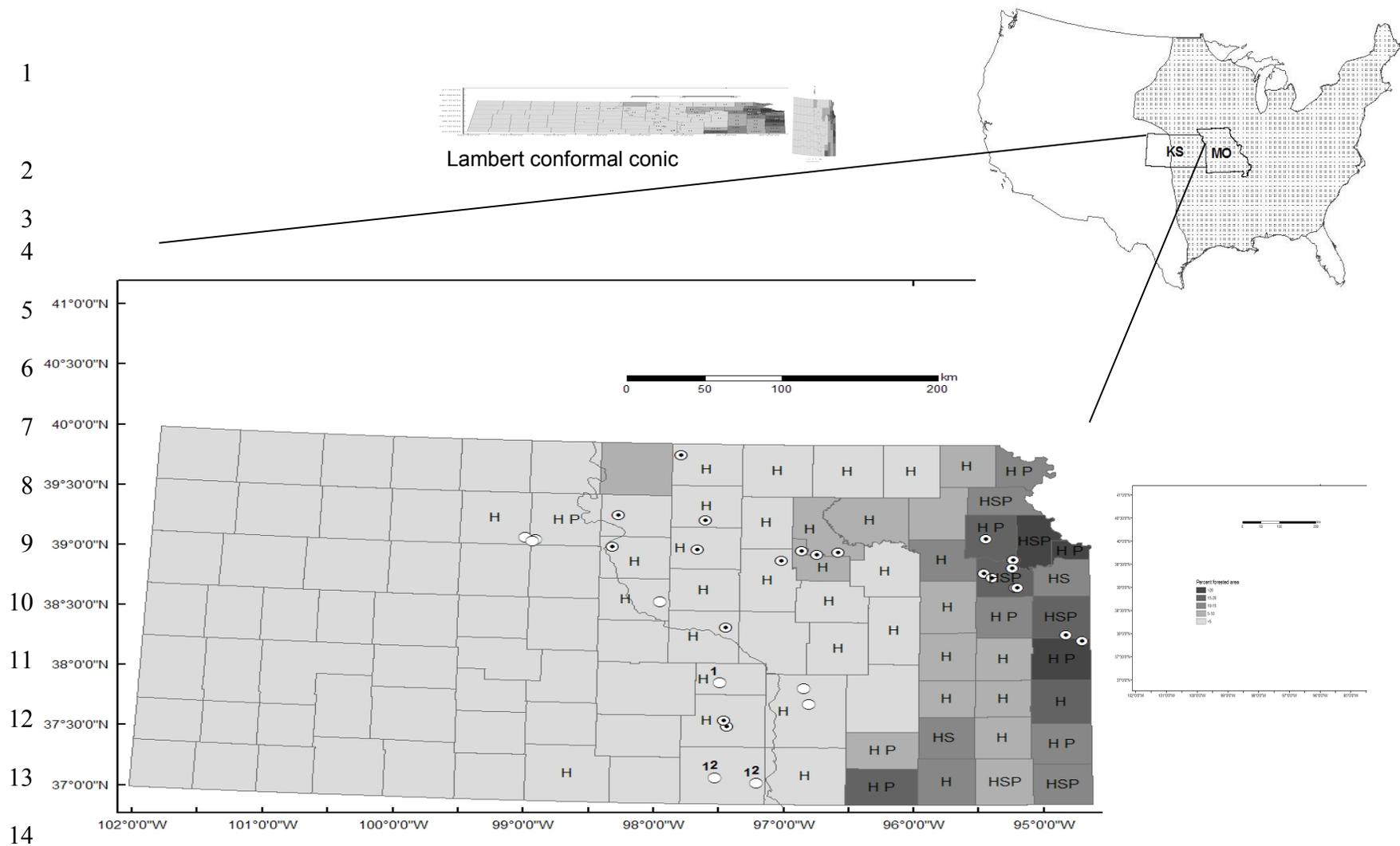
$\chi^2 = 10.3, \text{d.f.} = 2$

9

$p = 0.14$

$p = 0.006$

10



15 Fig. 1. Field and herbarium data displayed on map of KS, USA, with USA map showing distribution of *C. blanda*

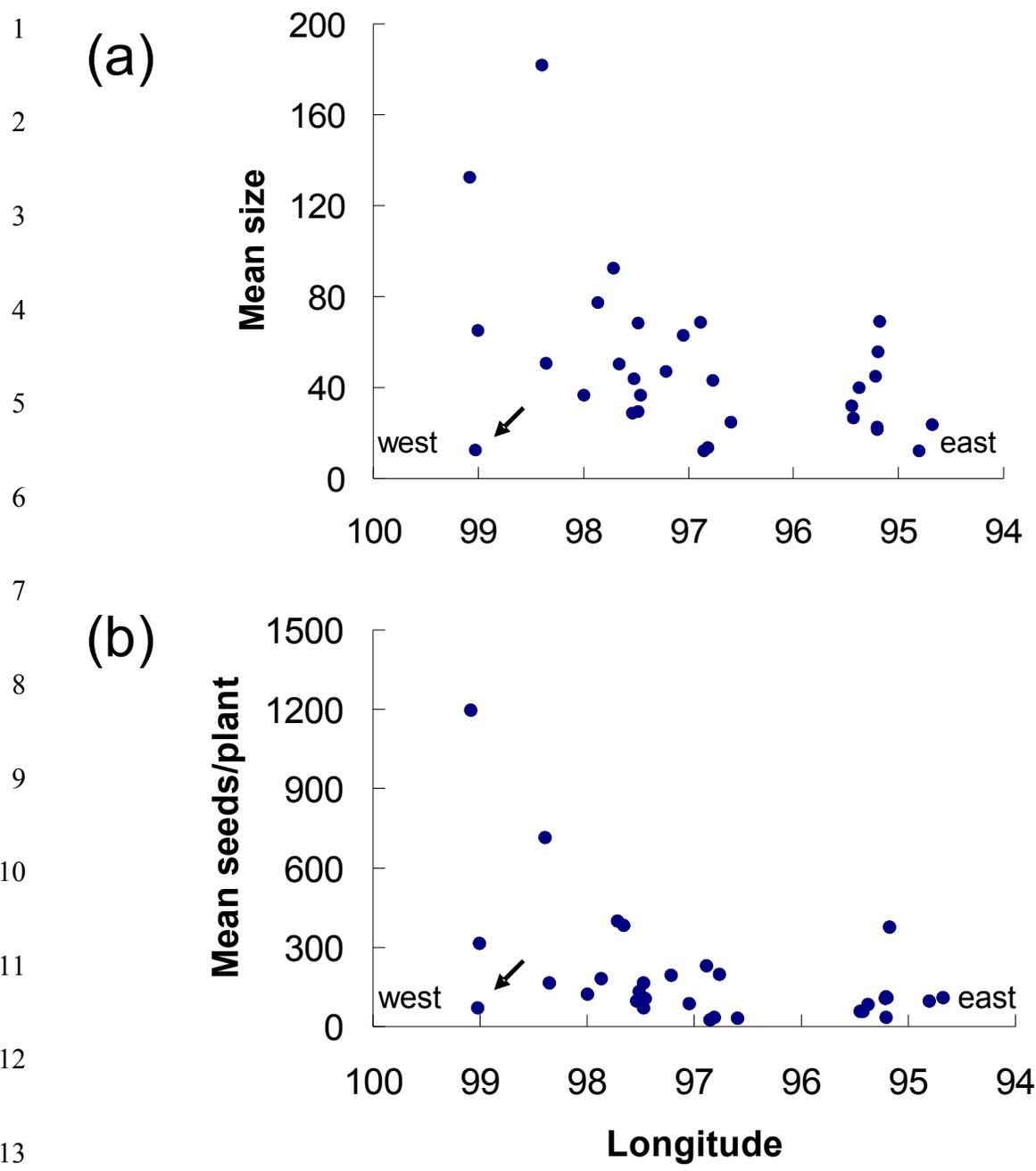
16 (<http://www.npwrc.usgs.gov/resource/othrdata/plntguid/species/careblan.htm>). The 31 field sites from 2005 are indicated by circles;

17 circles with or without a dot indicate locations where smut was present or absent, respectively. All sites had seed predators and rust

1with the exception of sites indicated along the western border with a 1 (seed predator absent) or a 2 (rust absent). The letters in the
2counties denote those in which the host plant (H), smut (S), or seed predator (P) occurred at least once in the herbarium dataset.
3Herbarium rust distributions are not shown, but nearly match the plant distribution (all but 4 counties with plants had at least one
4rusted specimen). Shading of counties reflects the percent of the county area in forest; see text. The line in central KS was digitised
5in a GIS from a scanned and georectified map of pre-European settlement vegetation by K uchler (1974), and indicates the western
6boundary of where prairies had a significant amount of ‘islands’ of forest vegetation.

7

8



15 Fig. 2. Relationship between individual plant traits and longitude for 31 KS field sites. a),
 16 average plant size (basal area, cm²), b) average seed production per plant. The arrows designate a

1site that was grazed; if this site is eliminated from the data, the positive relationship between
2plant traits and western longitude is stronger.

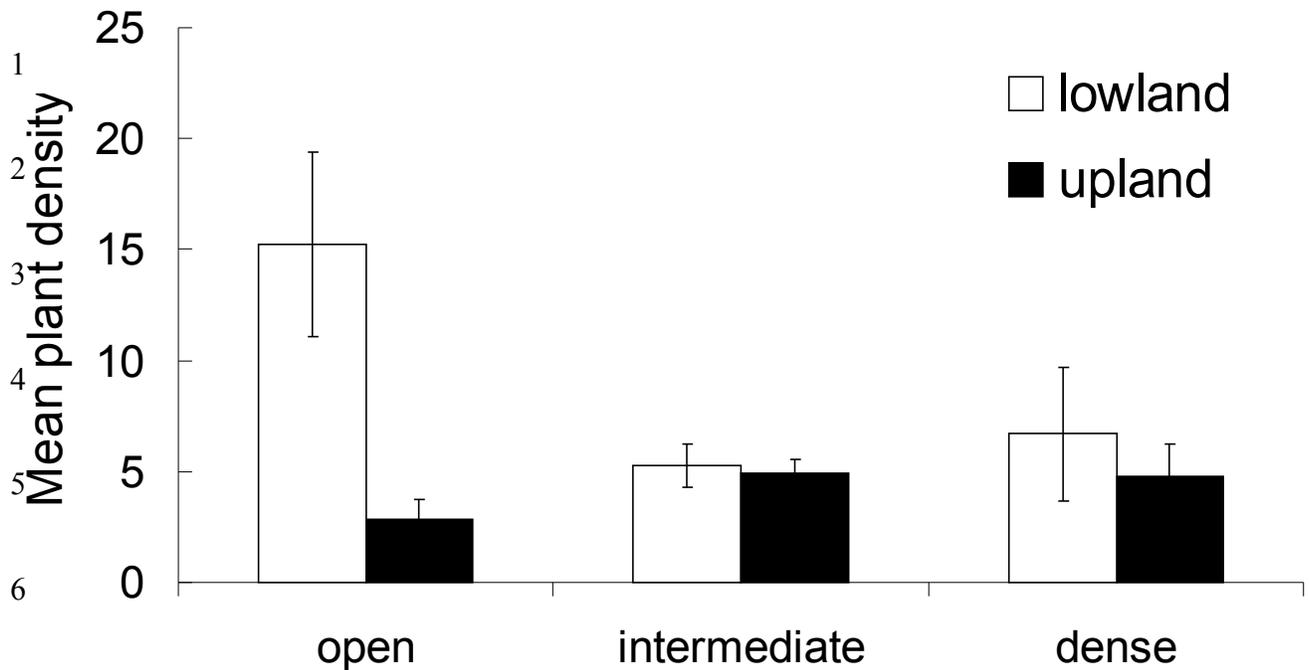


Fig. 3. Effect of habitat type (lowland vs. upland) and vegetation cover (open, intermediate, and dense) on average density (\pm standard error) of *C. blanda* in KS field sites. Average density of plants (\pm standard error) at sites. Significant terms in the analysis were Habitat ($F_{1,24} = 15.52$, $p < 100.001$), Cover ($F_{2,24} = 1.51$, n.s.), Habitat x Cover ($F_{2,24} = 10.07$, $p < 0.001$), and Survey date ($F_{1,24} = 9.40$, $p < 0.001$); $R^2 = 0.56$.

12

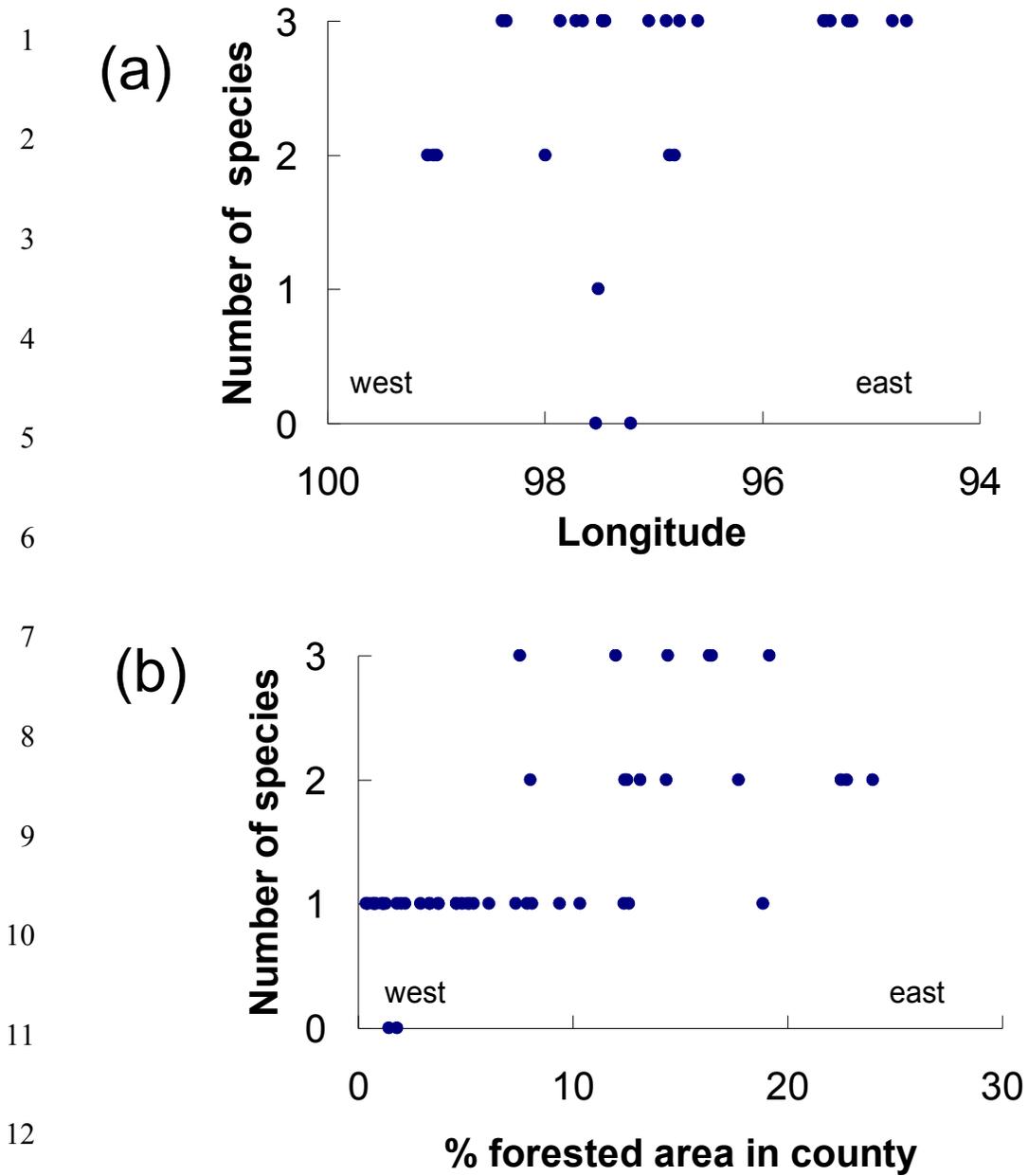
13

14

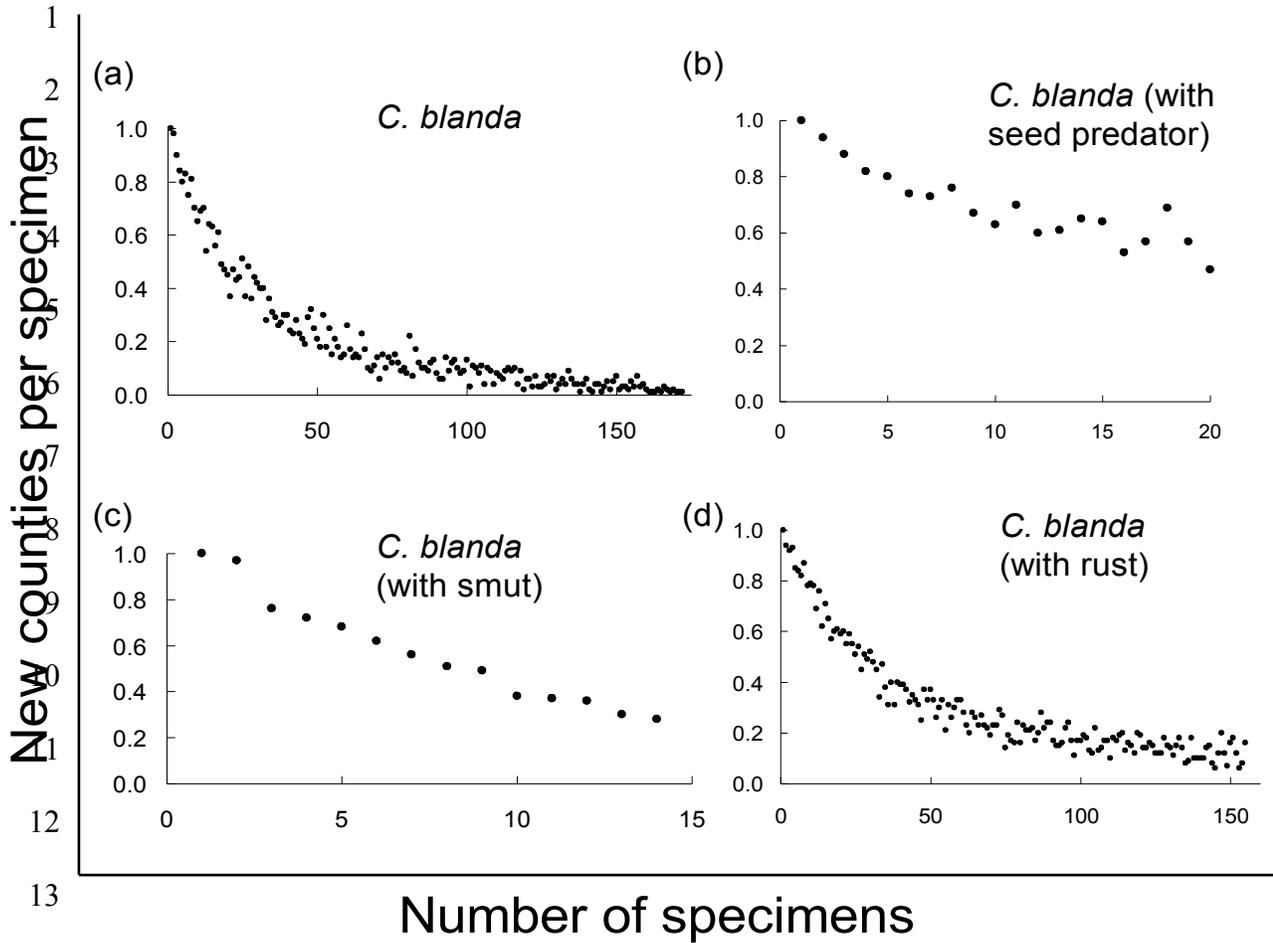
15

16

17



13 Fig. 4. Species richness of natural enemies of *C. blanda* in KS as related to a) longitude for field
 14 surveys and b) percent forest cover for herbarium surveys. For a), each point is based on a
 15 different field site in 2005 and for b), each point represents a county. A species richness of three
 16 indicates that the smut, seed predator, and rust were all found; smaller numbers represent
 17 situations where one or more of these species were not present.



15 Fig. 5. The probability of discovering a new county for each subsequent herbarium specimen
 16 examined for KS collections of a) *Carex blanda*, b) individuals of *C. blanda* infested by seed
 17 predators, c) individuals of *C. blanda* infected by smut, and d) individuals of *C. blanda* infected
 18 by rust. If most specimens are from unique counties, there is a high probability that examination
 19 of each subsequent specimen will expand the distribution, and curves will not reach the x axis.
 20 In contrast, if multiple specimens from the same county are common, curves will approach the x
 21 axis, as there is a lower probability that examination of an additional specimen will add new
 22 distributional information. See text and Antonovics *et al.* 2003 for details.