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Resource concentration dilutes a key pest in indigenous potato agriculture

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Abstract. Modern restructuring of agricultural landscapes, due to the expansion of monocultures and the resulting elimination of non-crop habitat, is routinely blamed for rising populations of agricultural insect pests. However, landscape studies demonstrating a positive correlation between pest densities and the spatial extent of crop monocultures are rare. We test this hypothesis with a data set from 140 subsistence farms in the Andes and find the inverse correlation. Infestations by the Andean potato weevil (*Premnotrypes* spp.), the most important pest in Andean potato agriculture, decrease with increasing amounts of potato in the landscape. A statistical model predicts that aggregating potato fields may outperform the management of Andean potato weevils by IPM and chemical control. We speculate that the strong pest suppression generated by aggregating potato fields may partly explain why indigenous potato farmers cluster their potato fields under a traditional rotation system common in Andean agriculture (i.e., "sectoral fallow"). Our results suggest that some agricultural pests may also respond negatively to the expansion of monocultures, and that manipulating the spatial arrangement of host crops may offer an important tool for some IPM programs.

Key words: Andean potato weevil; indigenous agriculture; monoculture; Peruvian Andes; potato; Premnotrypes *spp.; resource concentration hypothesis;* Solanum *spp.*

Introduction

Agricultural landscapes have been greatly simplified in the past century, due to the expansion of crop monocultures and the shrinkage of non-crop habitat, and this simplification is routinely blamed for rising populations of agricultural insect pests (Altieri and Letourneau 1982, Andow 1983, Matson et al. 1997, Naylor and Ehrlich 1997, Bianchi et al. 2006). Although several studies of agricultural landscapes have shown that the densities of some pests increase as the extent of non-crop habitat decreases, often because of decreased pest control services provided by natural enemies (Thies and Tscharntke 1999, Bianchi et al. 2006, Landis et al. 2008, Gardiner et al. 2009), landscape-scale studies directly demonstrating a positive association between pest densities and the extent of their hosts' monocultures are rare. At smaller spatial scales, this "monoculture" effect has been extensively tested in response to the resource concentration hypothesis (Root 1973), which predicts herbivore densities to increase with increasing densities of their host plants. Contrary to expectations, results from resource concentration studies suggest that monocultures result in lower pest densities just as often as they result in higher pest densities (Grez and Gonzalez 1995, Rhainds and English-Loeb 2003, Hamback and Englund 2005, Otway et al. 2005). In light of this, it is timely to revisit the assumption that the expansion of monocultures in agricultural landscapes invariably leads to upsurges in insect pest populations. Here we describe a landscape-scale test of the resource concentration hypothesis in 140 subsistence potato farms in the Andes.

Andean potato weevils (*Premnotrypes* spp.) are flightless, specialist insects, considered the most important pest of potatoes throughout the Andean region (Alcazar and Cisneros 1999). They are native to the Andes, where potatoes were domesticated roughly 5000 years ago. Under rain-fed agriculture, these weevils complete one generation a year, closely matching potato phenology (Alcazar and Cisneros 1999). Around the time when potatoes are planted, typically in October and November, adult weevils begin to emerge from their overwintering sites in the soils of previous-season potato fields and potato storage units, and walk to find their hosts (Alcazar and Cisneros 1999, Kroschel et al. 2009). Natural streams, which are common in Andean landscapes, are thought to inhibit their dispersal. When potatoes are found, weevils feed on their foliage and gravid females deposit their eggs on the base of the plants (Alcazar and Cisneros 1999). Following egg hatch, neonate larvae dig into the soil to burrow into potato tubers, where they feed to complete their larval

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development (Alcazar and Cisneros 1999). Toward the end of the season, in April and May, weevils begin to abandon tubers to pupate and later overwinter as adults in the soil. Larvae that mature before harvest emerge to pupate in the potato field. The remaining larvae are transferred within potato tubers to storage units, where they complete their development before emerging to pupate in the storage units' dirt floors. The relative fractions of weevils that overwinter in previous-season fields vs. storage units is still unknown, precluding practical landscape-level recommendations for their management. Partly due to the concealed habitat of their hosts, natural enemies of Andean weevils, all of them generalists, appear to be only modestly suppressive (reviewed in Kaya et al. 2009). Experimental augmentations of the enemies considered most promising (i.e., carabids, *Beauveria* sp., and *Heterorhabditis* sp.), yielding densities severalfold those encountered in nature, produced at best only modest weevil suppression in the field (Kaya et al. 2009).

Despite the development of an integrated pest management (IPM) program (Ortiz et al. 1996), farmers rely predominantly on insecticides to manage Andean potato weevils (Kühne 2007). Insecticide applications are cheap, but their use to manage potato weevils has been implicated in acute poisonings among Andean farmers at rates matching the highest reported anywhere in the world (Crissman et al. 1998, Cole et al. 2000). On the other hand, IPM tactics are safe but labor intensive, relying largely on reducing the pool of overwintering weevils, which are thought to be widely dispersed over the landscape, before they can immigrate into potato fields (Ortiz et al. 1996).

Our objective was to examine the practical significance of the resource concentration effect for subsistence farmers dealing with Andean potato weevils. To do so, we developed a multivariate landscape model to contrast the influence of resource concentration with the influences of chemical control and IPM on the weevils.

Materials and Methods

Study site

The study was conducted from November 2008 to May 2009 in four contiguous farming communities in the Peruvian Andes in the department of Huancavelica (Fig. 1; 74°45′ W, 12°46′ S). These communities belong to the Chopcca indigenous nation (see Plate 1), where agriculture is rain-fed and subsistence-based. The area is mountainous (3500–4200 m) and falls within a cold (6–12°C mean temperature) and semi-humid (500–1000 mm/yr rainfall) ecological zone, characteristic of highland agriculture in the Andes (Tosi 1960). Potato (*Solanum* spp.) is the most important crop, followed by barley (*Hordeum vulgare*), oats (*Avena sativa*), fava beans (*Vicia faba*), pearl lupine (*Lupinus mutabilis*), and minor quantities of other Andean crops. Farmers identify Andean potato weevils (*P. suturicallus*, *P. pierce*; see Plate 1) and potato flea beetles (*Epitrix* spp.) as their most important insect pests (S. Parsa, *unpublished data*).

Field sample

We selected four adjacent communities that covered the full elevation range in the region, from 3500 to 4200 m. Local authorities provided the roster of 643 total community members from which 157 farmers were randomly selected and one field per farmer was studied. Only pure plantings of the cultivars Yungay (improved, *S. tuberosum*) or Larga (landrace, *S. chaucha*) were included in the study, because they are the most abundant cultivars in the Chopcca nation and they are widely distributed in the Peruvian Andes. All farmers had fields of at least one of the two cultivars. When a farmer had fields of both cultivars, one was randomly selected for the study. We combined interviews and direct measurements to characterize management practices for each field from the day of planting until the day of harvest. To improve the quality of reports, soon after planting we provided farmers with record sheets for key future activities (e.g., pesticide applications, moundings of soil around the base of potato plants) and visited them at least twice during the season to collect the information. Only variables relevant to the agricultural landscape and pesticide use are drawn upon for the present study.

Response variable: Andean weevil infestations

To account for edge effects in Andean weevil infestations, which were observed during a preliminary study, fields were divided into two strata: edge and center. "Edge" was defined as the outer 3 m of the field, given that (1) it was not adjacent to a barrier putatively inhibiting weevil immigration (e.g., walls, channels, ditches > 1 m deep) and (2) it was not adjacent to another potato field. The remaining area of the field was considered "center." Based on this definition, 140 out of the 157 fields contained both strata and thus qualified for analyses relevant to the present study. From each stratum, 20 evenly distributed potato plants were harvested and their tubers combined. We categorized a tuber as "infested" when it displayed the external bruising characteristic of weevil damage. Therefore, we obtained two separate, albeit potentially correlated, estimates of weevil infestations per fields: one for edge and one for center.

Explanatory variables

Landscape features.—Using geographic positioning system receivers (GPSMap 76CSx; Garmin, Olathe, Kansas, USA) and geographic information system software (ArcGIS; ESRI, Redlands, California, USA), we mapped three landscape features in an area within 100 m of each field: current potato fields, previous-season potato fields, and potato storage units. The first is our measure of resource concentration, whereas the latter two are the putative sources of overwintering

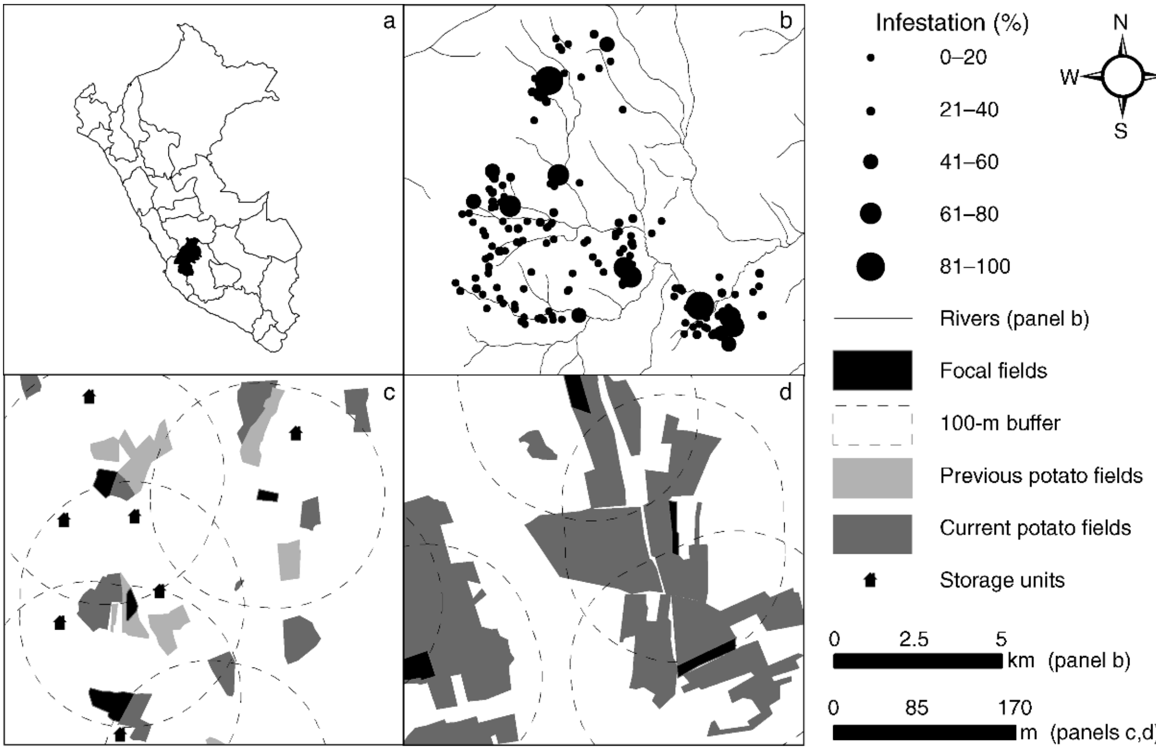

FIG. 1. (a) Map of Peru, showing the study area in the Peruvian Andes in the department of Huancavelica. (b) Distribution of focal fields in the study area, showing their percentage infestation (in the center stratum only) and the occurrence of major streams only (tributary streams are not included to avoid image saturation). The natural range in potato field concentration in our study area includes sites with (c) small and (d) large amounts of potato surrounding a focal field. To account for edge effects in Andean weevil infestations, fields were divided into two strata: edge (outer 3 m of the field without barrier to weevil immigration and not adjacent to another potato field) and center (remaining area of the field).

weevils. We considered the 100-m scale to be adequate, because weevils only disperse by walking, they have no mobile natural enemies that are effective, and the area considered often contained one or more natural streams. To afford a test of the potential influence of streams on weevil dispersal, we noted when a landscape feature was separated from the focal field by a stream, and used this criterion to generate "isolated" and "connected" variants for each landscape feature. Fields and storage units separated from the focal fields by a stream were considered to be functionally isolated from them, and they were hypothesized to bear no relationship to infestations. The opposite was true for features not separated from focal fields by streams, which we considered to be connected to them. Storage units were coded as counts, whereas fields were coded as the percentage of the total area within the 100-m buffer they occupied.

Insecticide treatments.—We asked farmers to report the date, product, and targeted pests of any insecticide treatment on their potato fields. We found very little variability in the product used (the organophosphate methamidophos applied with a backpack sprayer at roughly 534 mL of formulated active ingredient/ha) and targeted insects (Andean potato weevils and flea beetles jointly). However, we did find substantial variability in the number and timing of pesticide applications. To be most effective, chemical control must target adult weevils before they begin laying eggs, which occurs shortly after they immigrate to potato fields (Alcazar and Cisneros 1999). Because most immigration occurs before February (Kroschel et al. 2009), our explanatory variable was the total number of insecticide applications up to, but not including, February.

Statistical analysis

We used multilevel models fit with the lme4 package (Bates and Sarkar 2007) for R 2.9.1 with a binomial distribution for the dichotomous outcome variable for tuber damage (infested/uninfested) and a logit link (R 2.9.1 *available online*).[5] We considered field as a random effect to accommodate the lack of independence between edge and center infestations within a field, which were scored separately. The information-theoretic approach (Burnham and Anderson 2002) and Akaike's Information Criterion (AIC) were used to evaluate the multiple models explaining Andean potato weevil infestations.

[5] ⟨www.r-project.org⟩

TABLE 1. Summary statistics of variables used in model building of potato fields infested with the Andean potato weevil (*Premnotrypes* spp.) in the Peruvian Andes.

Variable	Mean ± SD	Range
Tubers sampled	330.9 ± 125.1	86–891
Tubers infested	62.4 ± 60.6	0–347
Storages connected	1.0 ± 1.0	0–5
Storages isolated	0.1 ± 0.4	0–3
Previous potato connected	4.0 ± 4.2	0–24.3
Previous potato isolated	0.5 ± 1.3	0–6.5
Current potato connected	8.1 ± 8.7	0–54.3
Current potato isolated	0.8 ± 2.0	0–17.0
Pesticide applications	1.6 ± 0.8	0–4

Notes: Storages are facilities, most typically within a farmer's home, where potatoes are stored after harvest. Current potato and previous potato are percentages of the area within 100 m of the focal plot where potatoes were sown during the current or previous planting season, respectively. Connected indicates the feature was not separated from the focal field by a stream, while isolated means that the focal field was separated by a stream.

We first evaluated the inclusion of potentially important covariates as control variables, considering their significance ($P < 0.05$) and improvements they afforded on model AIC values (>3). Based on these criteria, we included stratum as the sole control variable in addition to the random effect, leaving out cultivar, field area, and perimeter-to-area ratio. Then, we evaluated four competing landscape models to select the one that best explained our outcome variable. The four models considered were explicitly designed to (1) evaluate improvements in prediction when a measure of resource concentration was included and (2) test for the influence of streams on the landscape features being studied. Explanatory variables included in any given model were never strongly correlated ($|r| < 0.17$). To better guide our model selection, we calculated the relative probability of each model considered being the best one in the set using Akaike weights, w_i. Finally, we added the variable for insecticide treatments to the best landscape model from the previous step to evaluate its impact on the model and contrast its effect magnitude with that of the selected landscape variables.

We evaluated spatial autocorrelation in model residuals with the ncf package (Bjornstad 2004) for R, using the correlog( ) function to generate correlograms (Legendre and Fortin 1989) that tested for spatial autocorrelation at 250-m intervals. Correlograms plot Moran's I index on the y-axis and distance classes on the x-axis, allowing the assessment of autocorrelation with increasing distance. The correlog( ) function calculates Moran's I correlation coefficients at each distance and tests for significance with a permutation test, in our case, with 1000 permutations. Unless otherwise stated, mean values are presented with their standard deviation.

Early in the development of our model, we were concerned that the distribution of our resource concentration data was strongly skewed to the left. Rescaling these data with a square-root transformation fixed the distribution problem, but lowered the AIC by one relative to the percentage values. This suggested the original distribution did not bias our predictions, so we maintained percentage values for ease of interpretation and comparability with other studies. All results and conclusions in this study are qualitatively the same when square-root transformed data are used instead of percentage data.

RESULTS

Characteristics of focal fields

For each potato field, we evaluated an average of 331 ± 125 tubers in each of the two strata. The percentage of tubers infested with Andean potato weevils averaged 20.8% ± 19.7% (range: 0.0–86.6%). Fields were small, averaging 426.2 ± 286.2 m^2. The outer 3 m of each field, defined as edge, occupied on average 36.0% ± 18.9% of the field area, and experienced on average 7.9% greater infestations than the center. Focal fields were very often adjacent to other potato fields sown either by the same farmer (with a different potato cultivar) or by a neighboring farmer, most typically a family member. For this reason, the landscape within 100 m of focal fields was typically composed of more current-season potato fields than previous-season potato fields (i.e., 8.1% vs. 4.0%; Table 1).

Summary statistics for the explanatory variables are presented in Table 1. The area within 100 m of focal fields averaged 40 860 ± 3408 m^2, which conveniently helps us interpret 1% of this area as a rough equivalent of one potato field. To be precise, 96 potato fields of mean size could be sown within this area (40 860 ÷ 426 = 96.0). A stream was found within this area in 52.9% of the sampled fields ($N = 140$). These streams separated some previous potato fields from the focal field in 31 farms, current potato fields from the focal field in 37 farms, and storage units from the focal field in eight farms. The fraction of the landscape features separated by streams was low, suggesting that, although the spatial scale selected was adequate to capture the influence of our key landscape predictors, a larger scale may be necessary to test more definitively for the influence of streams.

Model development

Pest control advisors in the Andes typically voice a conceptual model of Andean weevil ecology that considers only the role of weevil sources (previous potato fields and storage units) as landscape features influencing infestations. Our quantitative version of this model, which we call the "null" model, suggests that potato storage units are more important sources of immigrating weevils than previous-season potato fields. Only storage units had a statistically significant influence on infestations, and, at their mean observed values, the influence of storage units was 2.6 times larger than the influence of previous-season potato fields. When the influences of resource concentration (i.e., current-season potato fields) and natural streams were also taken into

TABLE 2. Log-odds estimates ±SE for binomial models with landscape features predicting Andean weevil infestations.

Model	Null	Full	Connectivity	Connected
ΔAIC relative to null	0	−11	−9	−12
w_i	0.00	0.33	0.12	0.55
Storages connected			0.35 ± 0.11**	0.35 ± 0.11**
Storages isolated			−0.14 ± 0.30	
Storages total	0.30 ± 0.11**	0.28 ± 0.11**		
Previous potato connected			0.03 ± 0.03	0.04 ± 0.03
Previous potato isolated			−0.01 ± 0.09	
Previous potato total	0.03 ± 0.03	0.03 ± 0.03		
Current potato connected			−0.05 ± 0.01**	−0.05 ± 0.01**
Current potato isolated			−0.01 ± 0.06	
Current potato total		−0.05 ± 0.01**		

Notes: Lower AIC values suggest improvements in prediction relative to the model typically voiced by Andean pest control advisors (null model). The odds-ratio is the proportional increase in the odds of infestation for each unit increase of the explanatory variable. All models use a random effect for plot and a fixed effect for stratum as control variables (not included in the table).

** $P < 0.01$.

account, prediction was dramatically improved (Table 2). In fact, based on its Akaike weight, there was no probability that the null model could outperform any other model in the set. In all models considered, neighboring current potato fields had a negative and statistically significant association with infestations, and their inclusion offered the greatest improvements in AIC (Table 2). Adding only this explanatory variable to the null model (i.e., full model) reduced the AIC by 11. When landscape features were partitioned into their connected and isolated components (i.e., connectivity model) based on whether they were separated from focal fields by a stream, the AIC was penalized by two relative to the previous model, the estimates for the isolated components were small in magnitude relative to connected ones, and the direction of their association departed from expectations based on previous model results. These observations suggest that isolated components did not influence infestations. The best competing model (lowest AIC) was the one that considered only landscape features not separated from focal fields by streams (connected model). Based on Akaike weights, there was a 0.55 probability that this model was the best out of the set of competing models considered. Adding our explanatory variable for insecticide applications to the best landscape model reduced the AIC by two, and its parameter estimate had a negative and statistically significant association with weevil infestations (Table 3).

Pest control scenarios

The model incorporating landscape effects and pesticide applications (Table 3) was used to project the maximum levels of pest suppression obtained under three management scenarios. First, we calculated expected infestations for a hypothetical field untreated with insecticides and with mean observed values for neighboring storage units (i.e., 1.0 unit), current-season potato (i.e., 8.1%) and previous-season potato (i.e., 4.0%) (see Table 1). Under the IPM scenario, we calculated expected infestations if the farmer were to kill all weevils overwintering within 100 m of his field, such that previous-season potato fields and storage units were no longer sources of immigrating weevils (i.e., they are set to zero in the model). This is a best case scenario for Andean weevil IPM, which should be rather difficult to achieve by most farmers. Under the chemical control scenario, we calculated expected infestations if the farmer were to treat his field with insecticides four times (i.e., the maximum treatments observed; Table 1). Finally, under the resource concentration scenario, we calculated expected infestations if the farmer were to clump his field with other current-season potato fields, such that 54.3% of the area within 100 m of his field is composed of potato (i.e., the maximum percentage observed; Table 1). Using this approach, the model suggests that the resource concentration scenario offers the greatest pest suppression potential, followed by the chemical control scenario and then the IPM scenario (Fig. 2).

Controls and diagnostics

Model residuals were not spatially correlated at any of the distance classes tested (lowest P value > 0.4). The random effect standard deviation is 1.344, relatively large in comparison with other model coefficients. Thus, field-to-field heterogeneity in infestation rates, unex-

TABLE 3. Binomial model estimates when the variable "Pesticide applications" is added to the best landscape model (connected model) predicting Andean weevil infestations (Table 2).

Parameter	Estimate	SE	Odds	P
Intercept	−1.867	0.299	0.155	<0.001
Stratum (edge)	0.612	0.019	1.844	<0.001
Storage connected	0.365	0.113	1.441	0.001
Previous potato connected	0.032	0.028	1.033	0.243
Current potato connected	−0.040	0.014	0.961	0.004
Pesticide applications	−0.292	0.139	0.747	0.036

Notes: The random effect SD (1.344) is an indicator of the between-field variability not explained by the explanatory variables. ΔAIC (−14) indicates the extent to which this model is better than the null model (and all other models in Table 2).

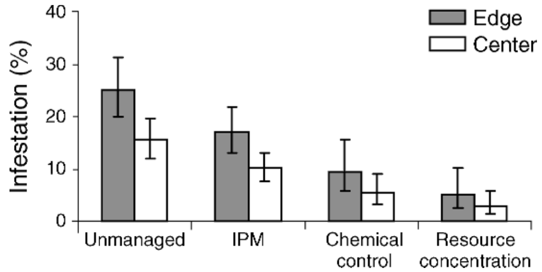

FIG. 2. Andean weevil management scenarios with predicted infestation (mean ± SE, $N = 140$ fields) based on the best-fitting statistical model. Predictions for the unmanaged scenario are based on mean amounts of weevil sources and neighboring potato fields with no insecticide treatments and are the starting point for subsequent treatments. Predictions for the IPM scenario are based on reducing the amount of weevil sources to zero. Predictions for the chemical control scenario are based on increasing insecticide use to four applications before February (the period when they are most effective against adult Andean potato weevils). Predictions for the resource concentration scenario are based on increasing the amount of neighboring potato to 54%.

plained by our explanatory variables, is an important feature of the data.

DISCUSSION

We observe a strong negative association between Andean potato weevil infestations and the abundance of potato in the agricultural landscape. This is the inverse of the pattern typically expected for the spatial dimension of the monoculture effect, or resource concentration, in agricultural landscapes. At smaller spatial scales, a negative response of herbivores to resource concentration has been observed in many studies (reviewed in Rhainds and English-Loeb 2003), and it was demonstrated for all specialist herbivores in a grassland biodiversity experiment (Otway et al. 2005). At the landscape level, however, we are aware of only one study demonstrating a similar correlation, which led the authors to advocate the clumping of host fields to reduce pest impact (Carriere et al. 2006). Our contribution here is to fully characterize the practical significance of this phenomenon from a pest management perspective.

We caution that our study only addresses the spatial dimension of the monoculture effect (i.e., potato clumping), leaving aside its temporal dimension (i.e., consecutive potato plantings at the same location) whose influence in our system is addressed elsewhere (Parsa 2009). When potatoes are not planted consecutively at the same location, as is the case here (farmers almost never plant a given field to two successive crops of potatoes), immigration may be the dominant process determining weevil densities at any given field. Our results suggest that fields that are "concentrated" exert a containment effect on weevil immigration by intercepting most immigrants on peripheral patches, releasing internal patches from pest pressures. We suspect that this containment effect may be an important factor limiting weevil populations over time, as each year the system is spatially "reset." However, a more definitive conclusion on how potato field concentration affects weevil populations over time requires a multiyear study.

Our results suggest that resource concentration is highly relevant to the management of Andean potato weevils. For example, the model described in Table 3 predicts that it would take only five farmers to aggregate their potato fields (approximately four mean size fields each) to halve their predicted weevil infestations. Furthermore, our model predicts that this aggregation alone could outperform IPM and chemical control as they are currently practiced by Andean farmers to manage Andean potato weevils.

The negative response of Andean potato weevils to resource concentration is larger and thus more readily extended to provide pest management solutions than the negative response of other pests to non-crop habitat. In their influential study, Thies and Tscharntke (1999) predicted that infestations by rape pollen beetles (*Meligethes aeneus*) would decrease by roughly 35% as the non-crop area increased from 3% to 50%. By contrast, over the same percentage increase in potato area, our model predicts weevil infestations to decrease by 81%. More importantly, our predictions are based on landscape composition within 100 m of focal fields, whereas Thies and Tscharntke's (1999) are based on landscape composition at a scale 7.5 times larger. This difference in spatial scales is important because as the functional scale for habitat management increases, so does the number of farmers who must coordinate their efforts to reap a joint return. Experiences in areawide IPM suggest that farmer coordination can be very difficult to achieve (Koul et al. 2008). Furthermore, from the perspective of habitat manipulation in pest management (Landis et al. 2000), manipulating resource concentration may be more advantageous than manipulating non-crop habitat because it does not require farmers to take land out of production.

The negative herbivore response to resource concentration found in our study is consistent with theoretical and empirical work in animal behavior showing that aggregation reduces predation risk ("selfish herding"; Hamilton 1971, Krause 1994). In a "selfish herd," individuals at the center of the herd are less vulnerable to attack than the individuals surrounding them (Hamilton 1971, Krause 1994). In a similar manner, aggregating potato fields may reduce infestation risk, because as weevils disperse to find potatoes they may be intercepted by peripheral potato patches. At a smaller spatial scale, this mechanism is evident in the strong edge effects produced by the weevils in our potato fields. In fact, this same mechanism often underlies the design of trap cropping systems in pest management (Shelton and Badenes-Perez 2005).

For many indigenous farming communities in the Andes, aggregating potato fields is in fact their

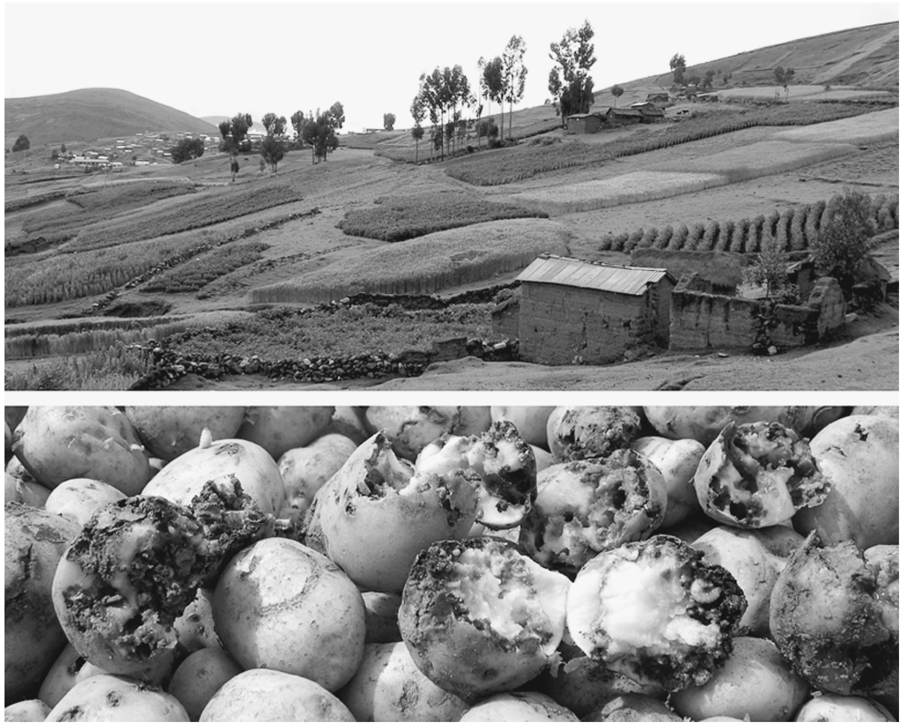

Plate 1. (Top) Agricultural landscape in the Chopcca indigenous nation and (bottom) potato tubers heavily infested by Andean potato weevils *Premnotrypes* spp. Photo credits: S. Parsa.

traditional practice. Under a rotation system known as sectoral fallow, all farmers in a community aggregate their fields in one sector in the landscape, essentially creating a large monoculture (Orlove and Godoy 1986). The location of the potato sector changes each year, with the previous potato sector often separated from a current potato sector by one or more streams over a distance larger than a kilometer (Parsa 2009). Recently, Parsa (2009) associated the replacement of this sectoral fallow system with a more diverse "mosaic" agricultural system with the rise of Andean weevils from noneconomic to key pest status. The present study was designed to characterize some of the mechanisms potentially involved. Our results strongly support a suppressive influence of potato field aggregation on Andean potato weevils. Our results also support, albeit more tentatively, the hypothesis that streams can act as barriers to Andean potato weevil dispersal (Parsa 2009), suggesting that, under the sectoral fallow system, streams may physically isolate overwintering weevils from potato fields. The negative response of weevils to resource concentration demonstrated here may partially explain the rationale behind the seemingly paradoxical formation of large monocultures in indigenous potato agriculture. We suspect that the evolution of sectoral fallow systems was partially favored by a selfish herding mechanism to reduce Andean potato weevil infestations.

Although we chose to contrast the benefits of resource concentration with those of commonly used management alternatives, its suppressive effect should best be seen as offering a refinement, not a replacement, to more comprehensive IPM programs. Our results suggest an additional tactic for Andean weevil IPM, by demonstrating that storage units are the most important sources of infestation, suggesting that farmers could gain substantial payoffs by targeting control practices to storage units. Judging by the strong effects demonstrated here, we suspect that manipulating the spatial arrangement of crops may offer important improvements for many IPM programs.

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