Contributed Paper

Effects of Vegetation Cover, Presence of a Native Ant Species, and Human Disturbance on Colonization by Argentine Ants

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Abstract: *The spread of non-native invasive species is affected by human activity, vegetation cover, weather, and interaction with native species. We analyzed data from a 17-year study of the distribution of the non-native Argentine ant* (Linepithema humile) *and the native winter ant* (Prenolepis imparis) *in a preserve in northern California (U.S.A.). We conducted logistic regressions and used model selection to determine whether the following variables were associated with changes in the distribution of each species: presence of conspecifics at neighboring sites, distance to development (e.g., roads, buildings, and landscaped areas), proportion of vegetation cover taller than 0.75 m, elevation, distance to water, presence of both species at a site, temperature, and rainfall. Argentine ants colonized unoccupied sites from neighboring sites, but the probability of appearance and persistence decreased as distance to development, vegetation cover, and elevation increased. Winter ants appeared and persisted in sites with relatively high vegetation cover (i.e., highly shaded sites). Presence of the 2 species was negatively associated in sites with high vegetation cover (more winter ants) and sites near development (more Argentine ants). Probability of colonization of Argentine ants decreased where winter ants were most persistent. At sites near development within the preserve, abundant Argentine ant populations may be excluding winter ants. The high abundance of Argentine ants at these sites may be due to immigration from suburban areas outside the preserve, which are high-quality habitat for Argentine ants. In the interior of the preserve, distance from development, low-quality habitat, and interaction with winter ants may in combination exclude Argentine ants. Interactions among the variables we examined were associated with low probabilities of Argentine ant colonization in the preserve.*

Keywords: edge effect, *Prenolepis imparis*, propagule pressure, vegetation cover

Efectos de la Cobertura Vegetal, Presencia de Especies de Hormigas Nativas y Perturbación Humana sobre la Colonización por Hormigas Argentinas

Resumen: *La expansión de especies invasoras no nativas es afectada por la actividad humana, la cobertura vegetal, el tiempo y la interacción con especies nativas. Analizamos datos de un estudio de 17 años de la distribución de la hormiga argentina no nativa (*Linepithema humile*) y la hormiga nativa (*Prenolepis imparis*) en una reserva en el norte de California (E.U.A.). Realizamos regresiones logísticas y utilizamos selección de modelos para determinar si las siguientes variables se asociaban con cambios en la distribución de cada especie: presencia de individuos de la misma especie en los alrededores, distancia a áreas desarrolladas (e. g., caminos, edificios y jardines), proporción de cobertura vegetal mayor a 0.75 m, altura, distancia al agua, presencia de ambas especies, temperatura y precipitación. Las hormigas argentinas colonizaron sitios no ocupados de sitios adyacentes, pero la probabilidad de aparición y persistencia decreció a medida que incrementó la distancia al desarrollo, la cobertura vegetal y la altitud.* Prenolepis imparis *apareció y persistió en sitios con cobertura vegetal relativamente amplia (i e., sitios muy sombreados). La presencia de las 2*

especies se asoció negativamente en sitios con amplia cobertura vegetal (menos P. imparis*) y en sitios con desarrollo (más* L. humile*). La probabilidad de colonización de* L. humile *disminuyó donde* P. imparis *eran más persistentes. En sitios cercanos al desarrollo, las abundantes poblaciones de* L. humile *pueden estar excluyendo a* P. imparis*. Al gran abundancia de* L. humile *en estos sitios se puede deber a la inmigración desde áreas suburbanas fuera de la reserva, que son hábitat de buena calidad para* L. humile*. En el interior de la reserva, la distancia a áreas desarrolladas, hábitat de baja calidad y la interacción con* P. imparis *combinadas puede excluir a* L. humile*. Las interacciones entre las variables que examinamos estuvieron asociadas con baja probabilidad de colonización de la reserva por* L. humile*.*

Palabras Clave: cobertura vegetal, efecto de borde, *Prenolepis imparis*, presión de propágulos

Introduction

Non-native invasive species reduce probabilities of persistence of native species in many communities and ecosystems (Sakai et al. 2001). Non-native ants, for example, disrupt ant communities and interspecific interactions in the areas they colonize (Holway et al. 2002; O'Dowd et al. 2003). The geographic spread of non-native invasive species and their effects on native species are associated with environmental covariates including vegetation cover, weather and climate, and human activity (Thomas & Holway 2005; Going et al. 2009; Kestrup & Ricciardi 2009). Human land use can facilitate invasive species' colonization of previously uninvasible areas (Menke & Holway 2006; Pauchard et al. 2009) or create conditions that allow invaders to exclude native species (MacDougall & Turkington 2005; Menke et al. 2007; King & Tschinkel 2008).

In a preserve in northern California (U.S.A.), we examined the effects of proximity to developed areas, weather, distance to water, elevation, proportion of vegetation cover taller than 0.75 m, and presence of a native ant species on site-level colonization by the Argentine ant (*Linepithema humile*) . The Argentine ant has invaded areas worldwide, especially in Mediterranean climate zones. Its global spread is associated with human activity, and in many invaded regions it inhabits primarily areas around human habitations (Suarez et al. 2001; Carpintero et al. 2003; Rowles & Silverman 2009). In arid regions, heat and low humidity limit spread (Menke & Holway 2006; Schilman et al. 2007), and Argentine ants have colonized natural areas only along riparian corridors or urban edges that receive water runoff (Suarez et al. 1998; Holway 2005; Holway & Suarez 2006). In more mesic regions, such as some parts of Hawaii, Argentine ants have colonized natural areas more extensively (Krushelnycky et al. 2005; Hartley et al. 2010) than in arid regions and spread is limited by cold temperatures, which hinder colony growth and reproduction (Hartley & Lester 2003; Abril et al. 2008). Argentine ants' moisture and temperature requirements may preclude colonization of uplands in some regions (Ward 1987) and forests in others (Krushelnycky et al. 2005; Ward & Harris 2005).

Where Argentine ants have colonized, few native ant species coexist with them (Holway et al. 2002; Carpin-

tero et al. 2007; Rowles & O'Dowd 2007). In California, however, the native winter ant (*Prenolepis imparis*) survives in areas colonized by Argentine ants (Ward 1987; Suarez et al. 1998; K. Fitzgerald, T. Sorrells, and D.M. Gordon, unpublished). Both species feed on honeydew produced by phloem-sucking insects (Nygard et al. 2008; Rowles & Silverman 2009). They coexist partly because their nesting and seasonal ecology differ. Argentine ants move nest locations frequently (Heller & Gordon 2006) and are most active in September (Suarez et al. 1998; Sanders et al. 2001). In contrast, winter ants live in deep, long-used nests and are not known to migrate to new nests (Tschinkel 1987). Their activity peaks during late autumn and early spring, and they often estivate during the summer, but specific timing of activities varies by location (Tschinkel 1987; Suarez et al. 1998; K. Fitzgerald, T. Sorrells, and D.M. Gordon, unpublished).

From 1993 through 2009, twice-yearly surveys of ant distributions were conducted at Jasper Ridge Biological Preserve (Santa Clara County, California), a 481-ha natural area owned by Stanford University, to track the colonization of the preserve by Argentine ants and the response of native ants to the colonization. When the survey began in 1993, Argentine ants already occupied many peripheral, low-elevation areas of the preserve (Human et al. 1998). The source of the ants in Jasper Ridge was suburban areas near the preserve. Between 1993 and 2001, Argentine ants progressively colonized the preserve in seasonal pulses. The invasion front progressed to new sites during summer and retreated during winter. In spring, the Argentine ants occupied fewer sites than the previous autumn (Sanders et al. 2001). These pulses reflected each colony's yearly cycle of expansion into a network of many small, ephemeral, and widespread nests in summer and their contraction into larger clusters of relatively permanent nests in winter (Heller & Gordon 2006).

Since 2001, few hectares of Jasper Ridge have been colonized for the first time, and summer expansions have been offset by winter contractions. Here, we examined the environmental variables associated with changes in distributions of Argentine and winter ants (*P. imparis*) since 1993. Taking into account the short dispersal distance of the Argentine ant, we investigated whether changes in Argentine ant distribution were associated with proximity to development (e.g., roads, buildings,

and landscaped areas); environmental variables (e.g., vegetation cover and elevation); presence of winter ants; and weather. We then investigated whether these variables and Argentine ant presence are related to changes in distributions of winter ants.

Methods

Ant Surveys

Jasper Ridge Biological Preserve (37°24′29″N, 122°13′39″W) is bordered by low-density suburban development, including buildings, farms, and roads; and the property itself contains a few buildings, parking lots, paved and dirt roads, and hiking and equestrian trails. It includes sections of San Francisquito Creek and its tributaries, including Searsville Lake and Dam. The preserve contains several different vegetation communities, including serpentine soil-based grassland dominated by native plant species, annual grassland dominated by non-native species, chaparral, coyote brush (*Baccharis pilularis*), and poison oak (*Toxicodendron diversilobum*) scrub, oak woodland, evergreen woodland, riparian woodland, and wetland.

We surveyed for ants twice yearly, in May and September, from May 1993 through September 2009. Survey points were arranged on a 100-m grid superimposed over the accessible areas (approximately 69%) of the preserve. We surveyed 334 points at least once and 121 points during all 34 surveys (mean of 25 [SD 11.6] surveys per point). In each survey, a 20-m radius around each point was searched once for 5 min. We identified all ants to genus. Through 1995 points with no ants were baited with honey traps for 24 hours (Sanders et al. 2001). Through 1996 ants were sometimes identified only as Argentine or native ants. For more information on survey methods see Human et al. (1998), Sanders et al. (2001), and Heller et al. (2008).

For each survey point, we used the Santa Clara County LIDAR (light detection and ranging) data set, which provides measures of ground elevation and vegetation height taken from an aircraft, to calculate the average elevation of the 1 ha surrounding the point and the proportion of the hectare covered by trees and shrubs (i.e., vegetation taller than 0.75 m). We used maps of Jasper Ridge and an aerial photograph to calculate the distance in meters from each survey point to the nearest water body and to the nearest developed area. Developed areas, clustered within the western portion of the preserve and along its boundary, included 7 buildings (field station, ranger residence, an art studio, an occasionally used horse stable, and several storage buildings), 3 gravel parking lots, trails, frequently traveled paved and gravel roads within the preserve, and the preserve boundary. We performed these calculations in ArcGIS (version 9.2., ESRI, Redlands, California) (additional details in Supporting Information).

Weather Data

We obtained data on precipitation and average minimum and maximum temperatures for each month between November 1992 and September 2009 from the PRISM Climate Group (2010). We averaged data from the 2 (4 km × 4 km) PRISM grid squares that overlap Jasper Ridge (centered at 37°24′59″N, 122°15′W and 37°24′59″N, 122°12′31″W). Following Heller et al. (2008), we calculated total rainfall and average minimum and maximum temperatures for each winter (November–April) and summer (May–September).

Analyses

Argentine ants spread with human assistance or on their own by budding, when a queen and workers walk to a new nest location (Suarez et al. 2001; Ingram & Gordon 2003). At Jasper Ridge, spread through budding predominates, with a maximum rate of 100–150 m/year (Suarez et al. 2001; DiGirolamo & Fox 2006), and longer-distance dispersal is limited to males during mating flights (Ingram & Gordon 2003). Because our survey sites were on a 100-m grid, a site was likely to be colonized only if Argentine ants were already present at 1 of the 8 neighboring sites, which were either 100 or 141 m away.

In analyses of species' invasions in which data are collected from sites arrayed in a grid, spatial autocorrelation may lead to spurious associations between variables associated with colonization and features of sites near other sites that are already colonized because probability of invasion may be associated with distance from conspecifics (Bini et al. 2009). We addressed autocorrelation by explicitly including the presence of Argentine ants at neighboring sites in our analyses. One of our fixed-effects variables was the proportion of surveyed neighboring sites at which Argentine ants were observed. We also examined whether environmental variables were associated with probability of persistence of Argentine ants at sites they had already colonized.

We used model selection to determine whether variables were associated with the appearance by Argentine ants at previously unoccupied sites and with Argentine ants' persistence at sites. We examined the changes in the presence of Argentine ants from each survey period to the next and from each survey period to the one in the same season the following year. We evaluated the weight of evidence for alternative models of 8 probabilities of transition, 4 from absence to presence of Argentine ants and 4 from presence to absence of Argentine ants. We examined probabilities of each of those 2 types of transition from spring to autumn in a given year ($n = 17$ years), from autumn of a given year to spring of the following year ($n = 16$), from autumn of a given year to autumn of the following year ($n = 16$), and from spring of a given year to spring of the following year ($n = 16$). In

each case, the binomial response variable was the presence or absence of Argentine ants in the second survey period.

We fit logistic regressions in R (version 2.10) (R Development Core Team, Vienna, Austria) with generalized linear mixed models (Bates & Maechler 2009). Models included random effects of site and year to account for repeated observations at the same sites. The fixed-effects variables were the proportion of surveyed neighboring sites in which Argentine ants were present during the first survey period in each comparison, the presence of winter ants at the site during the first survey period in each comparison, distance to development, proportion of the 1 ha surrounding the site covered with vegetation taller than 0.75 m, elevation, distance to water, rainfall, temperature, and the interactions among variables. Weather variables were included for the time between the 2 survey periods. Each model computed the probability (p) of Argentine ant presence at the next survey period, given the site and weather variables, with a logistic function, $p = 1/(1 + e^{-f(X)})$, where $f(X)$ represents a linear combination of the fixed and random effects.

To select the variables most strongly associated with appearance or persistence, we used forward selection with backward elimination and the Akaike information criterion (AIC) as the selection criterion (Burnham & Anderson 1998). This procedure selects the covariates most strongly associated with the response variables. We stopped adding variables when no new variables reduced the AIC by more than 2 because models with ΔAIC < 2 are generally considered equivalent (Burnham & Anderson 1998). When no new variables could be added, we added 2-way interactions for the selected variables (same procedure as for single variables). If, in a given step, the difference in AIC values of 2 models was <2, we continued model selection with both models in parallel. We were able to identify a single best model for each of the 8 probabilities of transition and did not perform model averaging. Because we used forward selection rather than exploring the entire model space, we did not calculate absolute ΔAIC.

To elucidate the effects of continuous variables and of interactions between winter ant presence and continuous variables on the transition probabilities, we graphed curves of the fitted models for each transition. We plotted the effect of each term in turn and held all other variables constant at their mean values. We computed the value of each variable at which the probability of appearance or persistence, as calculated by the logistic curve, was halfway between its minimum and maximum values.

We conducted the same analyses for winter ants as we did for Argentine ants, except that the first fixed-effect variable was the proportion of surveyed neighboring sites in which winter ants were present and the second was the presence of Argentine ants. We discarded data points when native ants at a site were not identified to species for either of the survey periods being compared.

Because Argentine ants and winter ants differ in seasonal activity, observations of the 2 species require slightly different interpretations. Argentine ants are active throughout the day and year (Human et al. 1998), so differences in occupancy from one survey period to the other probably reflect changes in local density of Argentine ants. In contrast, when winter ants were not observed during a survey period, especially in the autumn, they may have been present but estivating, so our data may underestimate their distributions. The data show the sites in which winter ants were present aboveground in the spring and autumn, the periods when encounters between the 2 species are most likely (K. F., T. Sorrells, and D. G., unpublished).

Results

Presence of Conspecifics at Neighboring Sites

Argentine ants were more likely to appear and persist at sites adjacent to those with Argentine ants (Figs. 1a & c). The proportion of neighboring sites with Argentine ants was the covariate most strongly associated with appearance and persistence and was the first or second selected variable for all 8 models (Table 1).

For winter ants, conspecific neighbors were less consistently associated with appearance and persistence than for Argentine ants. This variable was selected in 3 of 8 models. In the spring, winter ants appeared and persisted more often at sites that had many winter ant neighbors the previous spring or autumn (Table 2) than at sites with few conspecific neighbors.

Distance from Development

Argentine ants appeared and persisted most often at sites closest to developed areas (Figs. 1b & d). After proportion of neighboring sites with Argentine ants, proximity to development was the covariate most strongly associated with Argentine ant appearance and persistence and was the first or second variable selected in 7 of the 8 models (Table 1). From one autumn to the next, there was a weak interaction, selected last of 9 covariates, between distance to development and winter minimum temperature. As winter minimum temperatures decreased, the association between distance to development and persistence increased.

Distance to development was not associated with winter ant appearance or persistence. Proximity to developed areas was associated with appearance or persistence of winter ants only when Argentine ants were present. The negative association of Argentine ants with appearance at sites by winter ants decreased as distance from developed areas increased (Fig. 2a).
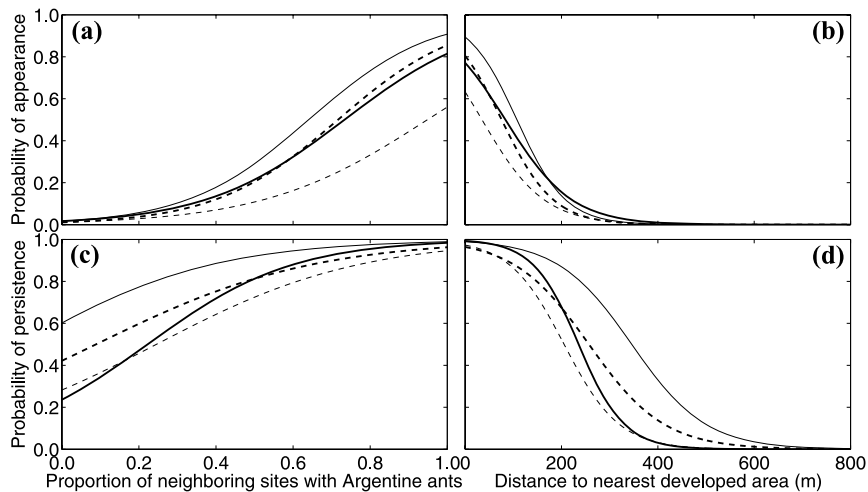
Figure 1. Seasonal patterns in effects of presence of Argentine ants in 8 neighboring sites on a grid and developed areas (buildings, roads, and landscaped areas) on probability of appearance and persistence of Argentine ants at a site: appearance of Argentine ants at previously unoccupied sites (a) as a function of proportion of 8 neighboring sites with Argentine ants, (b) as a function of distance to nearest developed area and persistence of Argentine ants, (c) as a function of proportion of 8 neighboring sites with Argentine ants, and (d) as a function of distance to nearest developed area (heavy solid lines, from one autumn to the next; light solid lines, from spring to autumn; heavy dashed lines, from one spring to the next; light dashed lines, from autumn to spring). Probabilities were calculated with the logistic functions computed for selected models (Table 1), and we assumed values of all variables were at their mean except the variable shown on the x-axis.

Vegetation Cover

As vegetation cover decreased, the probability of Argentine ant persistence increased. Logistic curves reached half their maxima when the proportion of cover taller than 0.75 m was 0.64–0.79, depending on season (Fig. 3a). Vegetation cover was moderately associated with persistence, selected second of 7, third of 5, fifth of 7, and third of 9 terms for the 4 models of persistence of Argentine ants (Table 1). Vegetation cover and elevation had a synergistic negative association with Argentine ant persistence. The negative association between closed canopy and persistence was mitigated with increasing winter rainfall. Vegetation cover itself was not associated with Argentine ant appearance. However, for appearance from spring to autumn the positive association with the presence of conspecific neighbors decreased as vegetation cover increased.

As vegetation cover increased, appearance and persistence of winter ants increased. Logistic curves reached half their maxima when the proportion of cover was 0.53–0.77, depending on survey period (Figs. 3b & c). Vegetation cover was most consistently associated with appearance and persistence of winter ants and was selected first in 7 of the models (Table 2). The interaction between vegetation cover and Argentine ant presence was selected in 3 of 8 models. The interaction strengthened the association of winter ants with vegetation cover in the presence of Argentine ants and weakened it in the absence of Argentine ants (Table 2 & Fig. 2b). Logistic

curves of the interaction terms reached half of their maxima when the proportion of cover was 0.64–0.69 in the presence of Argentine ants and 0.29–0.42 in their absence. From spring or autumn to the next spring, vegetation cover and proportion of conspecific neighbors were positively and synergistically associated with persistence of winter ants.

Elevation and Distance to Water

In general, appearance and persistence of Argentine ants increased as elevation decreased (selected second to last of 4, 4, and 8 variables in 3 of 8 models) (Table 1). Distance to water, which was highly correlated with elevation, was selected in only one model.

Similarly, the appearance and persistence of winter ants were not associated consistently with proximity to water or elevation, and these variables were selected in 1 of the 8 models. From autumn to spring, winter ants persisted more frequently at low-elevation sites, and the association between persistence and elevation increased as distance to water increased.

Presence of Other Species

Sites with winter ants had a lower probability of Argentine ant appearance and persistence (selected fourth of 8 and third of 7 terms in 2 of the 8 models). If only winter ants were observed at a site one autumn, Argentine

Table 1. Variables associated with changes in the observed distribution of Argentine ants in Jasper Ridge Biological Preserve in northern California (U.S.A.) after model selection.[a]

Argentine ant presence	No. data points (sites, compared periods)	AIC		Selected model					Beta coefficients of common covariates in selected models			
		random-effects model[b]	selected model[c]	log likelihood	no. parameters[d]	intercept	neigbbors[e]	development[f]	vegetation[g]	elevation[b]	winter ants[j]	vegetation :elevation[j]
Appearance												
spring to autumn within a year	2193 (274, 17)	1158	896	−441	7	−4.35	0.71 (2)	−2.22 (1)	–	−0.56 (3)	–	–
autumn of year x to spring of year x + 1	1836 (238, 16)	772	621	−306	5	−4.91	0.49 (2)	−2.45 (1)	–	–	–	–
spring of year x to spring of year x + 1	1837 (256, 16)	938	706	−346	7	−4.57	0.94 (2)	−1.89 (1)	–	−0.54 (3)	–	–
autumn of year x to autumn of year x + 1	1832 (233, 16)	1005	766	−372	11	−3.81	0.64 (2)	−2.02 (1)	–	–	−0.31 (4)	–
Persistence												
spring to autumn within a year	1724 (158, 17)	729	630	−305	10	4.42	0.77 (1)	−0.42 (3)	−0.79 (2)	–	–	–
autumn of year x to spring of year x + 1	1837 (177, 16)	1340	1218	−601	8	2.52	0.65 (2)	−0.75 (1)	−0.40 (3)	–	–	0.30 (5)

Table 1 (continued).

Argentine ant presence	No. data points (sites, compared periods)	AIC random-effects model[b]	AIC selected model[c]	Selected model log likelihood	Selected model no. parameters[d]	Selected model intercept	Selected model neighbors[e]	Selected model development[f]	Selected model vegetation[g]	Selected model elevation[b]	Beta coefficients of common covariates in selected models winter ants[i]	Beta coefficients of common covariates in selected models vegetation :elevation[j]
spring of year x to spring of year x + 1	1608 (157, 16)	1070	949	−464	10	2.81	0.74 (1)	−0.36 (2)	−0.39 (5)	-	−0.20 (3)	0.41 (6)
autumn of year x to autumn of year x + 1	1842 (173, 16)	96 7	805	−390	12	3.71	0.90 (1)	−0.68 (2)	−0.68 (3)	−0.33	-	0.43 (6)

Argentine ants were observed during the second but not the first of the 2 survey periods.
[a]*We used generalized linear mixed models with logistic response and conducted forward selection and backward elimination. We stopped adding variables when no new variables reduced the Akaike information criterion (AIC) by more than 2; this resulting model was the selected model. Using this procedure we were able to select a single model for each transition. Log likelihood, number of parameters, intercept, and coefficients are reported for selected models only. Coefficients were calculated with scaled variables, and scaling varied between comparisons of different survey periods; thus, coefficients should be compared only within a single transition. Numbers in parentheses beside coefficients indicate order in which terms were selected.*
[b]*Included only intercept and random effects of site and date.*
[c]*Selected with forward selection with backward elimination.*
[d]*Intercept and 2 random effects for every selected model and the selected variables and interactions.*
[e]*Proportion of surveyed neighboring sites with Argentine ants present during the first of the 2 survey periods.*
[f]*Distance to the nearest developed area within the preserve or at the boundary.*
[g]*Proportion of the site covered with vegetation taller than 0.75 m.*
[h]*Elevation of the survey site.*
[i]*Presence (1) or absence (0) of winter ants during the first of the 2 survey periods.*
[j]*Interaction between vegetation cover and elevation.*

Table 2. Variables associated with changes in the observed distribution of winter ants in Jasper Ridge Biological Preserve in northern California (U.S.A.) after model selection.[a]

Winter ant transition	No. data points (sites, compared periods)	AIC		Selected model				Beta coefficients of common covariates in selected models			
		random effects model[b]	selected model[c]	log likelihood	no. parameters[d]	intercept	vegetation[e]	Argentine ants[f]	neigh-bors[g]	Argentine ants: development[b]	Argentine ants: vegetation[i]
Appearing											
spring to autumn within a year	2910 (302, 17)	1266	1173	−579	8	−3.50	0.94 (1)	−0.84 (2)	–	0.55 (3)	0.34 (4)
autumn of year x to spring of year x + 1	3177 (293,16)	2798	2655	−1319	9	−1.64	0.95 (1)	−0.057 (3)	0.16 (2)	0.65 (5)	–
spring of year x to spring of year x + 1	2560 (288, 16)	2110	1973	−976	11	−1.73	0.90 (1)	−0.12 (3)	0.20 (2)	0.65 (7)	–
autumn of year x to autumn of year x + 1	3284 (292, 16)	1532	1454	−228	8	−3.14	0.90 (1)	−0.58 (3)	–	0.47 (4)	0.50 (5)
Persisting											
spring to autumn within a year	988 (232, 15)	922	862	−421	10	−1.78	0.63 (1)	−0.39 (2)	–	0.47 (6)	0.41 (5)
autumn of year x to spring of year x + 1	367 (142,16)	475	439	−210	10	0.04	0.66 (1)	–	–	–	–

continued

Table 2 (continued).

Winter ant transition	No. data points (sites, compared periods)	AIC random effects model[b]	AIC selected model[c]	Selected model log likelihood	Selected model no. parameters[d]	Selected model intercept	vegetation[e]	Argentine ants[f]	neighbors[g]	Argentine ants: development[b]	Argentine ants: vegetation[i]
							Beta coefficients of common covariates in selected models				
spring of year x to spring of year x + 1	802 (201, 15)	1044	973	−476	11	−0.09	0.60 (1)	-	0.26 (3)	-	-
autumn of year x to autumn of year x + 1	384 (141, 16)	474	459	−225	5	−1.05	-	-	-	-	-

Winter ants were not observed during the first date of the "appearing" transitions. They were observed during the first date of the "persisting" transitions.

[a]*We used generalized linear mixed models with logistic response and conducted forward selection and backward elimination. We stopped adding variables when no new variables reduced the Akaike information criterion (AIC) by more than 2; this resulting model was the selected model. Using this procedure we were able to select a single model for each transition. Log likelihood, number of parameters, intercept, and coefficients are reported for selected models only. Coefficients were calculated with scaled variables, and scaling varied between comparisons of different survey periods; thus, coefficients should be compared only within a single transition. Numbers in parentheses beside coefficients indicate order in which terms were selected.*

[b]*Model including only intercept and random effects of site and date.*

[c]*Model selected with forward selection with backward elimination.*

[d]*Parameters counted include intercept and 2 random effects for every selected model and the selected variables and interactions.*

[e]*Coefficient for the proportion of the site covered with vegetation taller than 0.75 m.*

[f]*Coefficient for the presence (1) or absence (0) of Argentine ants during the first date of the transition.*

[g]*Coefficient for the proportion of surveyed neighboring sites with winter ants present during the first date of the transition.*

[b]*Coefficient for the interaction between Argentine ant presence and the distance to the nearest developed area.*

[i]*Coefficient for the interaction between Argentine ant presence and vegetation cover.*
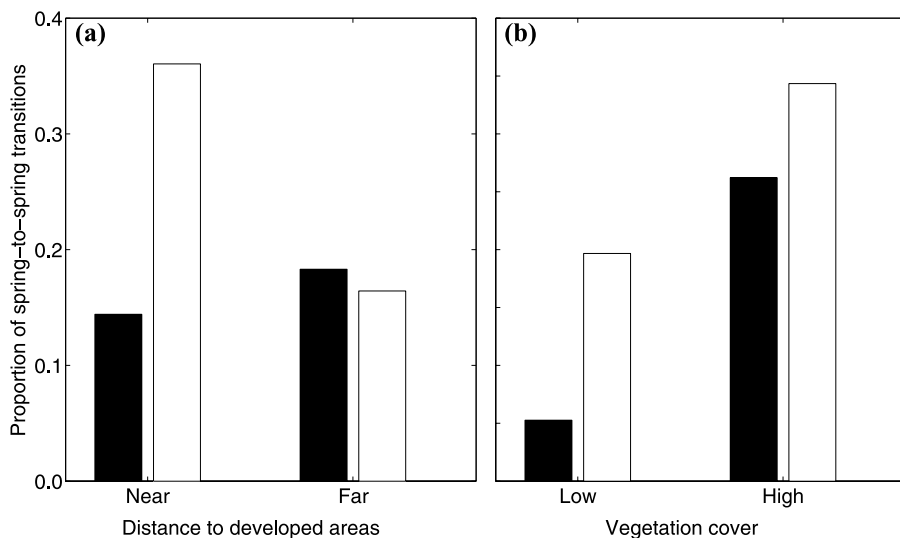
Figure 2. (a) Relation between winter ant appearance from one spring survey to the next and distance of site to developed areas as a function of the presence of Argentine ants. Bars show the proportion of transitions from one spring to the next in which winter ants appeared during the second spring of the paired surveys (black bars, sites with Argentine ants present during the first spring of the paired surveys; white bars, sites where Argentine ants were absent during the first spring of the paired surveys; near, 50% of sites closest to developed areas; far, 50% of sites farthest from developed areas). (b) Relation between winter ant appearance from one spring survey to the next and vegetation cover as a function of the presence of Argentine ants. Bars show the proportion of transitions from one spring to the next in which winter ants appeared during the second spring of the paired surveys (black, sites with Argentine ants during the first spring of the paired surveys; white, sites without Argentine ants during the first spring; low and high, respectively, sites in the lowest and highest quartiles of proportion of vegetation cover with height >0.75 m).

ants were less likely to appear at that site the following autumn (Table 1). Also, when both Argentine ants and winter ants were observed at a site during spring, Argentine ants were less likely to be present at that site the following spring (Table 1 & Supporting Information).

At sites where only Argentine ants were present, winter ants appeared less often in the next season or the next year than at sites without Argentine ants (Table 2). At sites where winter ants and Argentine ants were both observed in the spring, winter ants persisted until the autumn less often than at sites where only winter ants were observed (Table 2). However, negative associations of Argentine ants with appearance or persistence of winter ants decreased as distance to development increased, as proportion of vegetation cover increased, and as winter rainfall decreased (Table 2 & Figs. 2a & b).

Weather

Argentine ant appearance and persistence between one autumn and the next increased with increasing summer rainfall. This was the only weather variable that was associated consistently with changes in Argentine ant presence (selected third of 8 and fourth of 9 covariates, respectively, for models of appearance and persistence). The logistic curves reached half their maxima at 68 mm

of rainfall for appearance and 30 mm for persistence. Although temperature and its interaction with other variables were selected for several models, their effects were inconsistent and they were added late in the selection process.

For winter ants, as for Argentine ants, associations of appearance and persistence with weather variables were equivocal. Neither temperature nor rainfall was associated consistently with winter ant appearance or persistence.

Discussion

Human disturbance, habitat quality, and interactions with native species may affect the distributions of invasive species and effects on native species in preserves near developed areas. In our study, vegetation cover, elevation, presence of winter ants, and especially human disturbance were all associated with changes in Argentine ant distribution. Vegetation cover and distance to developed areas also affected the association between Argentine ant presence and appearance by winter ants (Fig. 3).

Invasions usually begin in areas of human activity, largely because propagules are first introduced in these areas (Sakai et al. 2001; Pyšek et al. 2010; Rizali et al.
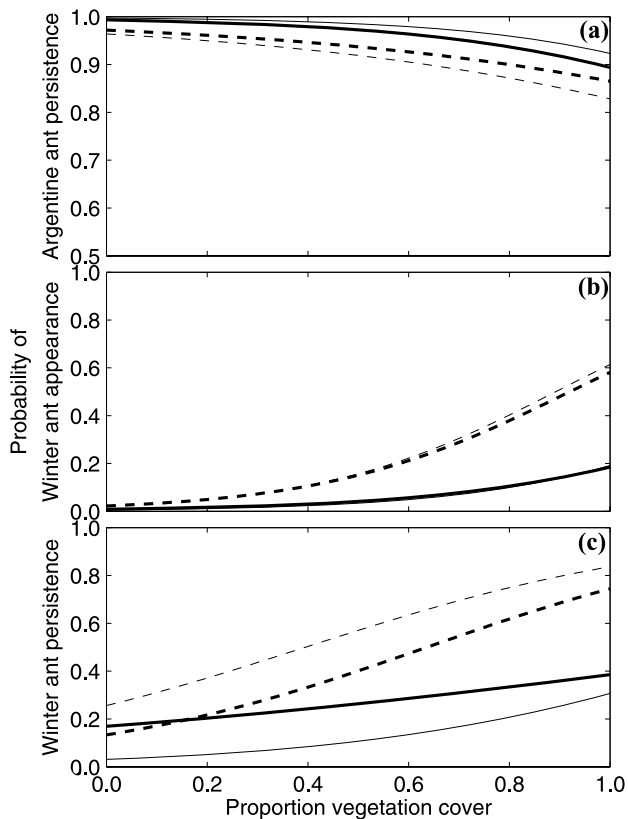
Figure 3. Seasonal patterns of association between vegetation cover with height >0.75 m and Argentine and winter ant appearance and persistence: effect of vegetation cover on the probability (a) that Argentine ants persisted at a site, (b) that winter ants appeared at a site, and (c) that winter ants persisted at a site (heavy solid lines, period from one autumn to the next; light solid lines, from spring to autumn; heavy dashed lines, from one spring to the next; light dashed lines, from autumn to spring). Probabilities were calculated with the logistic functions computed for selected models (Table 1), and we assumed values of all variables except vegetation cover were at their mean.

2010). At regional and global scales, Argentine ants are most successful in human-modified areas (Suarez et al. 2001; Roura-Pascual et al. 2011). In our study, Argentine ants rarely invaded sites far from development, even where they were present at neighboring sites. When they did invade such a site, they did not persist (Fig. 1d). Argentine ants' association with development was not due to opportunity only.

Rather, like other invasive species, including the fire ant (*Solenopsis invicta*) (MacDougall & Turkington 2005; King & Tschinkel 2008), Argentine ants may succeed in these sites because of human alterations to the physical environment. The effects of distance to development at Jasper Ridge may have been due to temperature rather than water limitations. In arid southern California, greater water availability in and near suburban areas increases the probability of invasions of Argentine ants (Suarez et al. 1998; Holway & Suarez 2006; but see Bolger 2007). In the more mesic environment of Jasper Ridge, changes in distributions of Argentine ants were not associated with distance from water, although they did spread more often in rainy summers, which is consistent with findings of Heller et al. (2008). That Argentine ant appearance and persistence were lower at higher elevation may have been due to lower water availability (Ward 1987) or cooler temperatures at these sites (Hartley et al. 2010). Proximity to developed areas was associated with Argentine ant persistence especially after cold winters. That Argentine ant persistence was lower at sites shaded by tall vegetation suggests they may be temperature limited at Jasper Ridge (Fig. 3a). Argentine ants do not occur in forested areas in Hawaii (Krushelnycky et al. 2005) and New Zealand (Ward & Harris 2005), probably due to cooler temperatures under the canopy. At Jasper Ridge, Argentine ants' winter nest aggregations occur at sunny sites (Heller & Gordon 2006); possibly they cannot find suitable winter nest sites in wooded areas, and migrate elsewhere or die during the winter.

Near Jasper Ridge, Argentine ants enter buildings during winter (Gordon et al. 2001), where warmer temperatures may lead to increased reproductive success (Hartley & Lester 2003; Abril et al. 2008). Argentine ants survive and reproduce outdoors at Jasper Ridge, but may do so at rates too low to expand their distribution without migration from surrounding developed areas. Bolger (2007) similarly proposed that the presence of Argentine ants near suburban edges of southern California natural areas is due to a source–sink dynamic in which ants migrate from high-quality, suburban habitat to low-quality less-developed habitat where they cannot sustain population growth (Fagan et al. 1999).

Winter ant presence was associated with lower Argentine ant presence for some survey periods. Winter ant presence may impede Argentine ant invasion at highly shaded sites that provide high-quality habitat for winter ants but low-quality habitat for Argentine ants. Winter ants were strongly associated with high levels of vegetation cover (Table 2 & Figs. 3b & c), which is consistent with their distribution throughout North American woodlands (Tschinkel 1987; Andersen 1997). In autumn surveys, they were mostly limited to shaded sites, and Argentine ants were less likely to appear the next autumn at these sites than at sites without winter ants. Presence of winter ants at sites in the spring was also associated with lower persistence of Argentine ants (Supporting Information).

Similarly, appearance of winter ants at sites with Argentine ants varied with season, vegetation cover, and development. In most survey periods, winter ants persisted at sites regardless of Argentine ant presence or absence

(Table 2), possibly because, like several other ant species that coexist with Argentine ants (Holway 1999; Holway et al. 2002; Sagata & Lester 2009), they produce chemicals to defend nests (Sorrells et al. 2011). Winter ant appearance, however, was negatively associated with Argentine ant presence in sites where Argentine ants were most persistent: near development or without thick vegetation cover (Figs. 2a & b).

Interactions with native species shape invasions mainly when the invading species is hindered by other factors (Levine et al. 2004; Ruesink 2007; Masciocchi et al. 2010). For ant invasions, in particular, resistance by native ants is usually ineffective (e.g., O'Dowd et al. 2003; Hoffmann & Saul 2010; reviewed in Lach & Thomas 2008); this is true of Argentine ant invasions (Holway 1999; Carpintero et al. 2007; Rowles & O'Dowd 2007). However, native competitors may kill small laboratory colonies of Argentine ants (Walters & Mackay 2005; Sagata & Lester 2009), and native ant communities slow, although do not prevent, invasions of Argentine ants in Southern California and Spain (Menke et al. 2007; Roura-Pascual et al. 2010). Sites in Europe with relatively many *Leptomyrmecine* genera are less likely to be invaded by Argentine ants, but this effect is mainly apparent at sites at the edge of the Argentine ant's climate tolerance where there is little human disturbance (Roura-Pascual et al. 2011).

If buildings contribute to rapid population growth of Argentine ants, then increased density of Argentine ants near developed areas may lead to the exclusion of native ants (Holway 1999; Walters & Mackay 2005; Sagata & Lester 2009). In some invasions, density reaches a critical mass (Roura-Pascual et al. 2010) that facilitates a wave of invasion (Von Holle & Simberloff 2005; Hollebone & Hay 2007; Clark & Johnston 2009). At Jasper Ridge, in contrast, it appears that a flow of migrants from developed areas has not helped Argentine ants overcome barriers to colonization (i.e., low-quality habitat and interaction with winter ants in the interior of the preserve). Thus, our results offer a local example of the regional pattern of Argentine ant invasion in Europe (Roura-Pascual et al. 2011). The distribution of an invasive species depends on habitat quality. At sites with low habitat quality, interactions with native species may prevent invasion, but human disturbance may change quality from low to high, and thereby alter the outcome of interactions between native species and invading species.

Acknowledgments

Supporting Information

Calculations of values of environmental variables in ArcGIS (Appendix S1) and a figure showing the association between presence of winter ants and Argentine ant persistence (Appendix S2) are available online. The authors are solely responsible for these materials. Queries should be directed to the corresponding author.

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