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Rainfall facilitates the spread, and time alters the impact, of the invasive Argentine ant

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Abstract Climate change may exacerbate invasions by making conditions more favorable to introduced species relative to native species. Here we used data obtained during a long-term biannual survey of the distribution of ant species in a 481-ha preserve in northern California to assess the influence of interannual variation in rainfall on the spread of invasive Argentine ants, *Linepithema humile*, and the displacement of native ant species. Since the survey began in 1993, Argentine ants have expanded their range into 74 new hectares. Many invaded hectares were later abandoned, so the range of Argentine ants increased in some years and decreased in others. Rainfall predicted both range expansion and interannual changes in the distribution of Argentine ants: high rainfall, particularly in summer months, promoted their spread in the summer. This suggests that an increase in rainfall will promote a wider distribution of Argentine ants and increase their spread into new areas in California. Surprisingly, the distribution of two native ant species also increased following high rainfall, but only in areas of the preserve that were invaded by *L. humile*. Rainfall did not have a negative impact on total native ant species richness in invaded areas. Instead, native ant species richness in invaded areas increased significantly over the 13 years of observation. This suggests that the impact of Argentine ants on naïve ant communities may be most severe early in the invasion process.

Keywords El Niño · Jasper Ridge Biological Preserve · *Linepithema humile* · Long-term · Seasonality

Introduction

Both climate change and invasive species alter the structure and function of native ecosystems, and their effects may interact (Dukes and Mooney 1999; Benning et al. 2002; Weltzin et al. 2003; Mooney and Hobbs 2005). Climate change associated with greenhouse gas emissions is altering temperature and precipitation as well as the magnitude and pattern of climate variation (IPCC 2007). Under different climate conditions, locations currently unfavorable to a particular invasive species may become more favorable (Kriticos et al. 2003; Peterson 2003; Roura-Pascual et al. 2004), and species coexistence and resource use may change (Levine and Rees 2004; Sanders and Gordon 2004), thus altering the susceptibility of communities to invasion (Chesson 2000; Davis et al. 2000; Cleland et al. 2004).

In the study reported here, we employed a long-term survey (1993–2005) of the distribution of ant species in a reserve in northern California to explore how interannual and seasonal variation in rainfall affects the rate of spread of invasive Argentine ants and their impact on native ant species. Experimental manipulations have shown that

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increases in water availability can affect the invasibility of communities (Harrington 1991; Dukes and Mooney 1999; Davis and Pelsor 2001; Menke and Holway 2006), and some long-term studies have shown that the abundance of invasive species can increase in years of high rainfall (Burgess et al. 1991; Hobbs and Mooney 1991) or in years with early warm temperatures (Stachowicz et al. 2002).

The Argentine ant, *Linepithema humile*, has been introduced and continues to spread in many regions around the world, often with devastating impacts on biodiversity and ecosystem function (reviewed in Holway et al. 2002a). The rate of spread of *L. humile* populations can vary considerably across habitats, seasons, and years (Way et al. 1997; Sanders et al. 2001; Suarez et al. 2001; Krushelnycky et al. 2004; DiGirolamo and Fox 2006). Rainfall is likely to influence the invasion dynamics of *L. humile*. Its nest distribution is limited by soil moisture availability in some locations (Ward 1987; Holway 1998; Holway et al. 2002b), and its abundance in pitfall traps increases in years with high rainfall (DiGirolamo and Fox 2006) and in areas with high soil moisture (Holway et al. 2002b; Menke and Holway 2006). Menke and Holway (2006) experimentally manipulated soil moisture and found that Argentine ants spread further along irrigated than along control transects in native ant communities in southern California. Due to frequent nest relocation and reproduction by budding (Heller and Gordon 2006), the response of Argentine ants to changes in rainfall can be rapid (Menke and Holway 2006) compared to that of other ant populations (i.e., Kaspari and Valone 2002).

Jasper Ridge Biological Preserve (JRBP), a 481-ha preserve in northern California, has been surveyed twice yearly since 1993, in May and September, to monitor distributions of Argentine ants and other ant species (Human et al. 1998; Sanders et al. 2001; Sanders et al. 2003; Heller et al. 2006). In the course of this long-term study, we have examined several aspects of the Argentine ant invasion, including seasonal and annual patterns in their rate of spread (Human and Gordon 1996; Sanders et al. 2001), abiotic correlates of their distribution (Human et al. 1998), their interactions with native arthropods and impact on native ant community organization (Human and Gordon 1997; Human and Gordon 1999; Sanders et al. 2001; Sanders et al. 2003), and the effect of their colony organization, including seasonal polydomy and reproduction by budding (Heller and Gordon 2006) on dispersal (Ingram and Gordon 2003) and rate of spread (Heller et al. 2006). The long-term data show that *L. humile* has continued to invade new areas in JRBP since 1993. However, its rate of expansion into new areas has varied considerably across years, and the distribution within JRBP contracted in some years because the ants abandoned some previously invaded areas. In the study reported here, we explored the influence of natural variation in rainfall on the long-term pattern of distribution and range expansion of Argentine ants in JRBP. We predicted that *L. humile* would spread more in years of high rainfall because higher soil moisture would increase both nest site availability and food supply and promote colony growth and that increased expansion would lead to a decrease in the activity and distribution of native ant species. We asked: (1) is interannual variation in the distribution of *L. humile*, and its rate of expansion into new areas, influenced by interannual variation in rainfall? (2) is the interannual variation in the distribution of three native ant species influenced by interannual variation in rainfall? (3) do rainfall and time, measured by time since the survey began in 1993, affect the richness of native ant species in areas invaded by *L. humile*?

Methods

Study system

Jasper Ridge Biological Preserve (JRBP) is located in northern California (San Mateo County, 37°24′N and 122°13′30″W, 67–207 m a.s.l.). Thirteen distinct habitat types occur in JRBP, including serpentine and annual grassland, chaparral, oak woodland, wetland, riparian, and evergreen and redwood forest (http://jrbp.stanford.edu). The JRBP is surrounded on all sides by low-density development, agriculture, and open space, much of which is invaded by *L. humile*.

Ant survey

This study used data obtained from surveys of the distributions of native ant species and *L. humile* in JRBP made each May and September from 1993 to 2005. In 1993, the 481-ha JRBP was divided into 1-ha quadrats using an aerial photograph. Argentine ants form large compound colonies consisting of many nests linked by trails (Markin 1968; Holway and Case 2000; Heller and Gordon 2006) that cover spatial areas up to approximately 1000 m^2 (Heller 2005). Some quadrats were not surveyed due to dense poison oak (*Toxicodendron diversilobum*) or other vegetation, flooding, or the presence of a lake. In the center of each accessible 1-ha quadrat, a 20-m radius circle (referred to as a ‘sample plot’) was searched for 5 person-min, and the presence of native ant species and *L. humile* was recorded. Sampling techniques included searching under rocks, scanning trees and vegetation, and sifting through leaf litter (methods applied in Human et al. 1998; Sanders et al. 2001). Previous studies at JRBP compared the results of this sampling method to both pitfall trapping (Human and Gordon 1996) and to more intensive searches at a finer scale (Sanders et al. 2001) and found no difference in the number of species detected, although some differences were found in which species were detected. The survey methods may overlook cryptic and rare species, but reliably detect conspicuous, active species that forage above the leaf litter (Bestelmeyer et al. 2004), including *L. humile* and the three native ant taxa discussed below.

On an average, 255 (range 169–310) sample plots were searched in each survey. In all surveys, except May and September 1993 and May 1996, native ants were identified to species or genus level. All surveys were conducted by graduate students with the help of undergraduate assistants. From 1993 to May 1996, surveys were managed by K. Human; from September 1996 to 1999 by N. Sanders; from May 2000 to 2004 by N. Heller; in 2005 by J. Shors. There was no significant difference among people managing the survey in terms of the mean number of species found per sample plot (ANOVA, $F_{3,44} = 0.81$, $P = 0.50$).

Climate data

Data on precipitation and temperature were collected from the JRBP weather station (37°23′12′′N, 122°14′26′′W). The site has a Mediterranean-type climate, characterized by cool wet winters (November–April) and warm dry summers (May–September). On an average, 96% of the annual rainfall occurs in the winter months. The timing and quantity of rainfall is strongly variable across years, marked by periodic years of highly abnormal rainfall, often in response to the El Niño southern oscillation (ENSO) (Schoner and Nicholson 1989). In the 1990s there was a series of El Niño/La Niña events, including the 1997–1998 El Niño, which is the strongest on record, producing a 100% increase in rainfall throughout California (Chagnon 2000). Annual precipitation at the site from 1992 to 2005 is shown relative to the 30-year average in Fig. 1.

Ant community

Thirty-one ant species have been collected at JRBP, of which 13 are detected frequently in our biannual ant survey (see Appendix 1 in the Electronic Supplementary Material). Voucher specimens are stored at the Bohart Museum at the University of California, Davis. Here we examine patterns of species richness in invaded plots over time, which includes data from all 31 ant species. In addition, we focus on the distributions of *L. humile* and three native ant species which were observed frequently in our survey and which are active across the range of temperatures in which the surveys were conducted (Human et al. 1998): (1) *Prenolepis imparis*, (2) *Formica moki*, and (3) *Tapinoma sessile*. *Prenolepis imparis*, the winter ant, is a common ant species throughout North America (Creighton 1950). Despite high diet overlap with *L. humile* (K. Barton, unpublished data; Lynch et al. 1980), it co-occurs with *L. humile* more frequently than do other native ant species in JRBP (Human and Gordon 1996; Sanders et al. 2001) and elsewhere (Tremper 1976; Ward 1987; Holway 1998; Suarez et al. 1998), perhaps because *P. imparis* is most active in the winter months when *L. humile* is less active (Ward 1987). At JRBP, *P. imparis* is active throughout the year in riparian and woodland areas, and in both the May and September surveys it remains the most common ant species that overlaps with *L. humile* (Sanders et al. 2001). *Formica moki* is the next most likely to co-occur with *L. humile* in JRBP, both in May and September, and it is very common in areas of the reserve in which *L. humile* is absent. The activity of *F. moki* peaks in the summer, like that of *L. humile* (Human et al 1998). *Formica moki* was sometimes not distinguished from *Formica subpolita* in the survey data. *Formica subpolita* is restricted to chaparral habitat at JRBP. To exclude *F. subpolita* from data for *F. moki*, we removed 21 survey plots in chaparral habitat from the analysis. The colonies of *T. sessile*, like those of *L. humile*, relocate nests in response to changes in resource availability, and this ant rapidly increases in abundance in response to irrigation (Menke and Holway 2006).

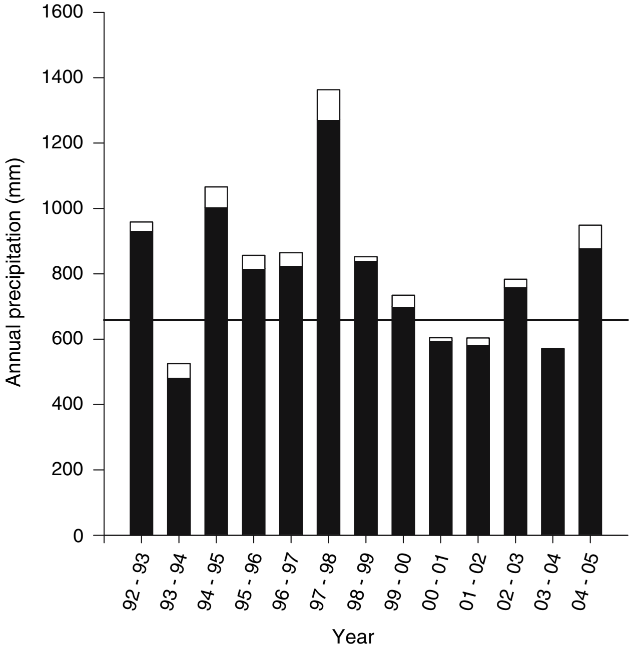

Fig. 1 Annual total precipitation at the Jasper Ridge Biological Preserve (JRBP), California from October 1992 to October 2005. Winter precipitation (*black bars*) occurs from October to April, and summer precipitation (*white bars*) from May to September in the year indicated. The *horizontal line* shows the 30-year average of annual precipitation

Distribution of ant species and rainfall

To examine the influence of rainfall on the interannual variation in the distribution of ant taxa, we used data from the 185 sample plots that were sampled in every survey between 1993 and 2005 in which native ants were identified to the species or genus level (1994–1995, September 1996, 1997–2005). We divided these 185 plots into two categories: *Invaded*, the 130 sample plots that were invaded by *L. humile* in at least one survey from 1993 to 2005, and *Intact*, the 55 sample plots that were never invaded.

We tested for an association between rainfall and the distribution of the ant species in May and September using stepwise multiple regression. We modeled the effects of four different rainfall variables: (1) rainfall in the winter preceding a survey (same year winter), (2) rainfall in the winter in the year before a survey (previous year winter), (3) rainfall in the summer in the year before a survey (previous year summer), and, for September data only, (4) rainfall in the summer directly preceding a survey (same year summer). Winter and summer precipitation in the same year were strongly positively correlated ($r = 0.75$, $P = 0.003$), but in some years winter rainfall was very low and summer rainfall was high (i.e., 1993–1994; Fig. 1), so we included them as separate effects.

For all four ant species studied (*L. humile*, *P. imparis*, *F. moki*, *T. sessile*), we estimated interannual changes in distribution as the change from year t to year $t + 1$ in the number of sample plots occupied. The response variable in all analyses was the total number of occupied sample plots in each survey for each species, not whether a particular sample plot was invaded or intact. Therefore, the response variable is not subject to spatial autocorrelation. The response of native ant species to rainfall was evaluated separately in *Invaded* and *Intact* plots because their response to rainfall may be influenced indirectly by the effect of rainfall on *L. humile*. We used stepwise multiple regression analyses that included each of the four rainfall variables listed above as independent factors, and interannual changes in distribution of ant species as dependent factors.

For each ant species, we selected the best-fit model by calculating all possible models and then selecting the model with the highest F statistic, lowest Akaike information criterion (AIC) score, and variance inflation factors lower than 1.5. Each final fitted model was tested to ensure the validity of the equation and suitability of the parametric regression approach. Residuals were examined for normality (Shapiro–Wilk W test, $P > 0.15$ for all) and constant variance. Durbin–Watson tests indicated that none of the models showed a serial correlation in error terms (Table 1; $P > 0.05$ for all).

Time-series data analyzed parametrically with regression are sensitive to violations of the assumption of independent random errors. While the data did not show serial correlation, to ensure the validity of our results we also used EcoSim ver. 7.0 (Gotelli and Entsminger 2006) to conduct separate randomization-based regressions between each rainfall variable and each ant distribution variable, including range expansion and species richness (described in following section). The randomization method does not depend on Gaussian assumptions and instead compares the observed correlation coefficient with a probability distribution of correlation coefficients generated by re-shuffling the data 1000 times. The results of these analyses were qualitatively similar to those generated by linear regression models and are, therefore, not reported further.

Range expansion of *L. humile* and rainfall

To study how rainfall influences the rate of range expansion of *L. humile*, we examined the relationship between the number of sample plots invaded by *L. humile* for the first time during our survey and the four winter and summer rainfall variables, using stepwise regression as described above. We considered newly invaded sample plots as range expansion for two reasons. First, the impact of Argentine ants on the structure and diversity of the native ant community occurs when an area is first invaded (Sanders et al. 2003). Second, because Argentine ants invaded new sample plots and abandoned others in the same year, overall change in interannual distribution may not reflect the numbers of newly occupied sites where impact is high.

In this analysis, we included all years of data and the 245 sample plots for which there were no gaps in sampling prior to invasion and we could therefore clearly infer when the invasion first occurred. We included time since the survey began as a predictor variable in the stepwise regression model to test if there were directional trends in invasion rate over time. Since slight autocorrelation occurred in the best-fit model for the September data (Durbin–Watson statistic = 1.34), we transformed both the independent and dependent variables using the Cochrane–Orcutt procedure to estimate parameters for linear regression (Cochrane and Orcutt 1949).

Native ant species richness, rainfall, and time since survey began

In each survey, native ant species were found in some of the invaded sample plots. We expected that in years of high rainfall, native ant species richness in these plots would decrease due to the suppression of native ant activity by increased *L humile* activity. We examined the relationship between mean native ant species richness across invaded plots and the four winter and summer rainfall variables using stepwise regression, as described above. To test for

Table 1 Results of stepwise multiple regression best-fit models for interannual distribution of ant species in September and May surveys

	Predictor variable				Model		
	Precipitation						
	Same year		Previous year				
	Summer	Winter	Summer	Winter	R^2	P value	Durbin–Watson
September							
Invaded plots							
Linephitema humile	+ 0.47**		+ 0.21*		0.61	0.01	1.73
Tapinoma sessile	+	–			0.43	0.10	1.63
Prenolepis imparis			+		0.15	0.24	2.61
Formica moki	+**				0.71	0.001	2.31
Intact plots							
T. sessile		–			0.05	0.51	1.83
P. imparis		+			0.17	0.20	2.48
F. moki	+				0.06	0.47	2.63
May							
Invaded plots							
L. humile			–		0.08	0.39	2.19
T. sessile	–				0.05	0.53	1.67
P. imparis			+*		0.52	0.02	1.97
F. moki			+		0.19	0.20	2.60
Intact plots							
T. sessile		–			0.16	0.26	1.46
P. imparis			+		0.11	0.34	2.90
F. moki			+		0.006	0.82	2.96

$^*P < 0.05$, $^{**}P < 0.01$

Predictor variables with (+) or negative (−) coefficients noted. For significant models, partial r^2 values are shown

changes in the impact of *L. humile* on native ant species richness over time, we also included time since the survey began as a predictor variable in the stepwise regression.

In this analysis, we calculated the mean native ant species richness for the subset of sample plots in which *L. humile* was found when the survey was started in 1993 and in which native ants were always identified to species ($n = 95$). Data on the presence of any of the 31 native ant species occurring at the preserve (Appendix 1 of Electronic Supplementary Material) were included in the calculation of the mean. If only *L. humile* was detected in a plot, the species richness value for that plot was zero. Data from both surveys in 1993 and the May 1996 survey were not included because native ants were not identified to species. September data were logarithmically transformed so that residuals were normal random variables.

Results

Distribution of ant species and rainfall

The distribution of *L. humile* in September was greater following high rainfall. Interannual variation in the spatial distribution of *L. humile* in September was best predicted by a model that included both same year and previous year summer rainfall ($R^2 = 0.61$, $n = 12$, $P = 0.01$). Same year summer rainfall explained the majority of the variation in the model (Table 1; Fig. 2a). Same year winter rainfall also predicted a significant amount of variation in the distribution of *L. humile* in September ($R^2 = 0.40$, $n = 12$, $P = 0.03$; Fig. 2b), but it did not enter the best-fit regression model because winter and summer rainfall in the same year are highly correlated. In contrast to September, the distribution of *L. humile* in May was not significantly related to any of the rainfall variables (Table 1).

For some native ant species in some seasons, distributions also depended on high rainfall, but only in *Invaded* sample plots. The best-fit model for the distribution of *P. imparis* in *Invaded* plots in May included previous year summer rainfall ($R^2 = 0.52$, $n = 11$, $P = 0.02$). There was no effect of rainfall on *P. imparis* distribution in September or in *Intact* plots (Table 1). The best-fit model for the distribution of *F. moki* in *Invaded* plots in September included same year summer rainfall ($R^2 = 0.71$, $n = 12$, $P = 0.001$). There was no effect of rainfall on *F. moki* distribution in May surveys or in *Intact* plots (Table 1). The distribution of *T. sessile* did not depend on rainfall in either season (Table 1).

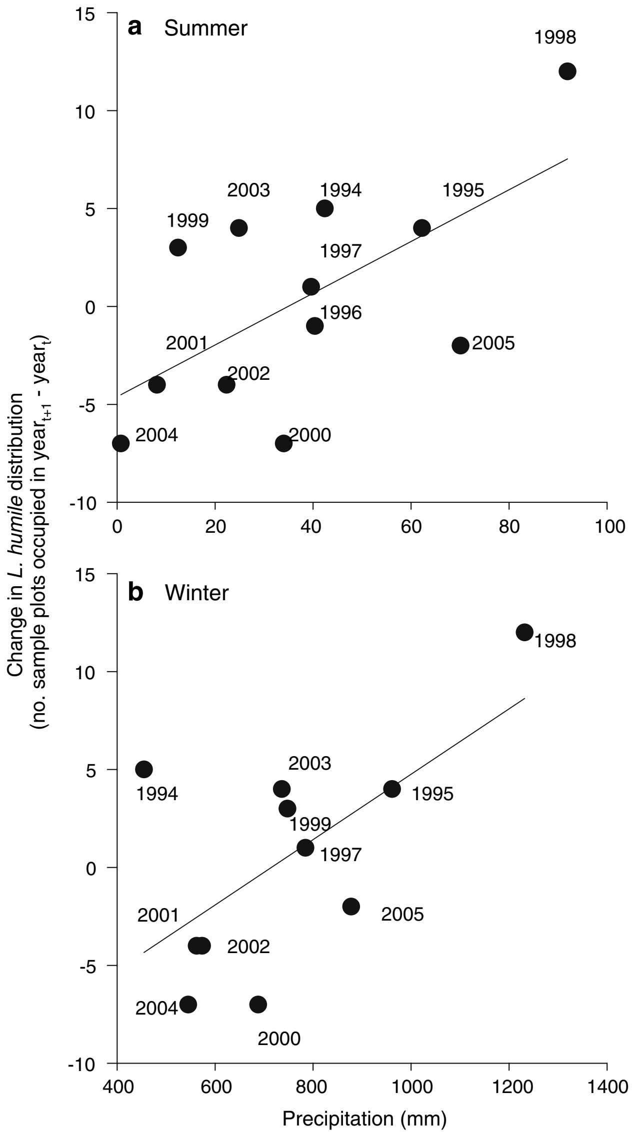

Fig. 2 Interannual change in the distribution of *Linepithema humile* in September from 1993 to 2005 as a function of same year precipitation in summer (**a**) ($r^2 = 0.40$, $P = 0.03$) and winter (**b**) ($r^2 = 0.40$, $P = 0.03$) in the same year, with best-fit regression lines

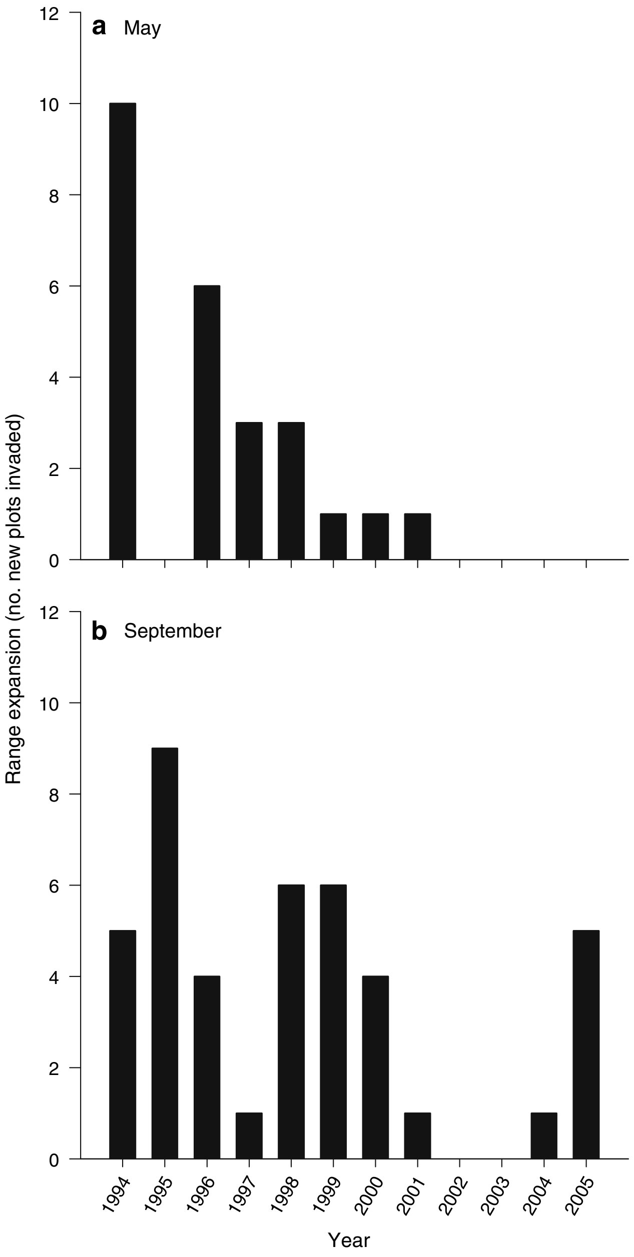

Fig. 3 Range expansion of *L. humile* from 1994 to 2005, measured as the number of newly invaded sample plots in each May and September survey

Range expansion of *L. humile* and rainfall

Argentine ants expanded into approximately 74 new sample plots over the 12 years of the survey (Fig. 3). In September, the rate of range expansion showed a trend toward a decline over time ($R^2 = 0.28$, $n = 12$, $P = 0.08$), but was more strongly associated with interannual variability in rainfall. The best-fit model for September data included same year and previous year summer rainfall ($R^2 = 0.59$, $n = 12$, $P = 0.02$; Fig. 4a), with same year summer rainfall explaining the majority of the variation (Table 2). The effects of winter rainfall on range expansion in September were less clear. The year of 1994 was detected as an outlier value (outlier analysis, JMP ver. 6.0) in the analysis with same year winter rainfall (Fig. 4b). Argentine ants expanded into many new plots in September 1994 when winter rainfall was the lowest of the 13 years but summer rainfall was relatively high (Fig. 4a). When we removed 1994 from the analysis, the best-fit stepwise regression included only same year winter precipitation ($R^2 = 0.47$, $n = 11$, $P = 0.01$).

In May, by contrast, rainfall had little effect on the rate of range expansion and, instead, the rate of range expansion significantly declined over time (Fig. 3). The best-fit model

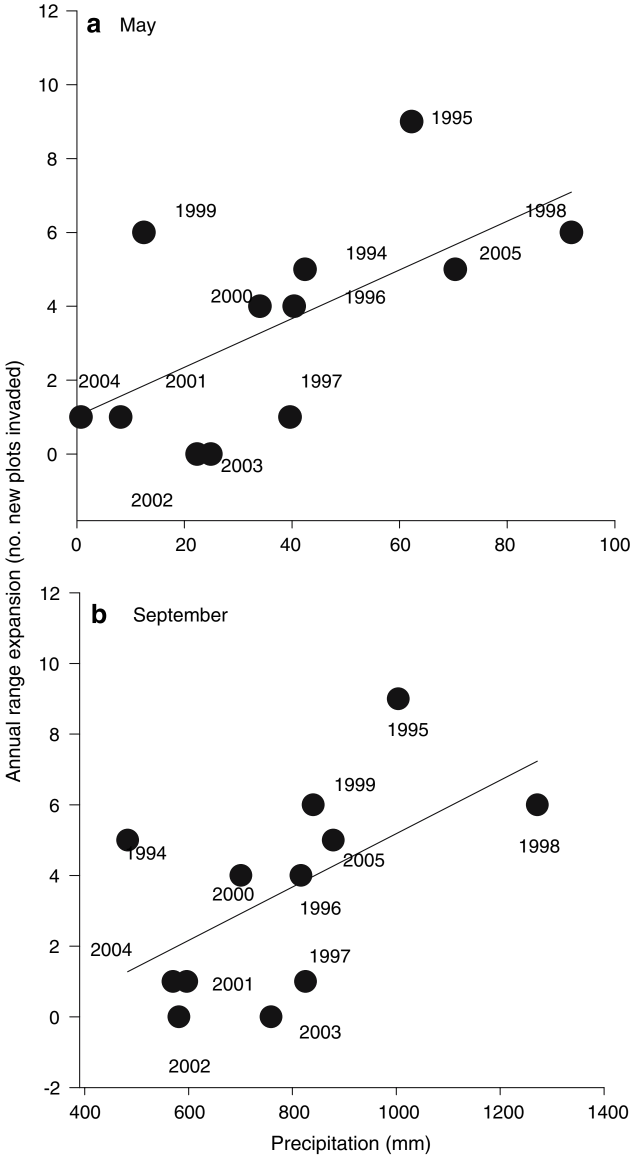

Fig. 4 Annual range expansion of *L. humile* in September as a function of same year precipitation in summer (**a**) ($r^2 = 0.38$, $P = 0.03$) and winter (**b**) ($r^2 = 0.30$, $P = 0.07$)

included time since the survey began and same year winter rainfall, with time since the survey began explaining most of the variation ($R^2 = 0.59$, $n = 12$, $P = 0.02$; Table 2).

Native ant species richness, rainfall, and time since survey began

Fewer native ant species were detected in *Invaded* plots (0.20 ± 0.41) than in *Intact* plots (1.57 ± 0.62) (*t* test, $t_{42} = 10.44$, $P < 0.001$). Native ants were found less frequently in September than in May in *Intact* plots (1.3 ± 0.18 for September, 1.9 ± 0.79 for May; $t_{20} = 2.1$, $P = 0.04$) and in *Invaded* plots (0.07 ± 0.05 for September, 0.28 ± 0.07 for May; $t_{20} = 8.2$, $P < 0.001$).

Native ant species richness in the subset of 95 plots invaded since the start of the survey tended to increase over time. In the later years of the survey compared to the early years, there were more plots with native ant species and *L. humile* found together, and there were more plots with more than one native ant species and *L. humile* found together. Mean native ant species richness in May significantly increased with time since the beginning of the survey ($R^2 = 0.47$, $n = 11$, $P = 0.02$; Fig. 5). The best-fit model for May data included time since the survey began, previous year summer rainfall, and same year winter rainfall ($R^2 = 0.83$, $n = 11$, $P < 0.01$; Table 2). In September, the best-fit model included same year summer rainfall and time since the survey began, but the model was not significant (Table 2; Fig. 5).

Discussion

Rainfall appears to influence the spread of Argentine ants, presumably through effects on soil moisture availability. Between 1993 and 2005, Argentine ants increased their range in JRBP. Their distribution and rate of expansion was highly variable from year to year (Sanders et al. 2001; Heller et al. 2006). Here we found that the spread of Argentine ants during the summer was strongly related to interannual variation in rainfall patterns. The distribution of *L. humile* in September, relative to the previous September, increased following wet weather and decreased following dry weather (Fig. 2), and *L. humile* invaded more new areas following high rainfall (Fig. 4).

Although annual rainfall influenced the spread of Argentine ants in summer, it was not associated with spread from one May to the next. Range expansion from one May to the next tended to decrease from 1993 to 2005, and there was no trend in rainfall over those years. In the early years of the survey, beginning in 1993, the range of *L. humile* expanded from one spring to the next, but since 2001 no new sample plots were invaded in May (Fig. 3). The total number of invaded sample plots in both May and September has also remained relatively constant since about 2000 (see also Fig. 2, Heller et al. 2006).

Rainfall cycles at longer time scales appear to influence the invasion. Argentine ant colonies are seasonally polydomous; in the winter groups of nests linked by trails contract to form large aggregations, and in the spring and summer these aggregations break apart and disperse (Heller and Gordon 2006). Worker production peaks from August through October (Markin 1970). Ants spread both in the winter, apparently by establishing new winter aggregations, and in the summer, by dispersing nests from the winter

Table 2 Results of stepwise multiple regression best-fit models for Argentine ant range expansion and native ant species richness in invaded plots

	Predictor variable					Model		
	Precipitation				Time			
	Same year		Previous year					
	Summer	Winter	Summer	Winter		R^2	P value	Durbin–Watson
Range expansion								
September	+ 0.45*		+ 0.21			0.59	0.02	1.73
May		− 0.09			− 0.55**	0.59	0.02	2.65
Native ant species richness								
September					+	0.35	0.15	1.83
May	− 0.04	+ 0.24**			+ 0.67**	0.83	< 0.01	1.80

$*P < 0.05$, $**P < 0.01$

Predictor variables with positive (+) or negative (−) coefficients noted. For significant models, partial r^2 values are shown

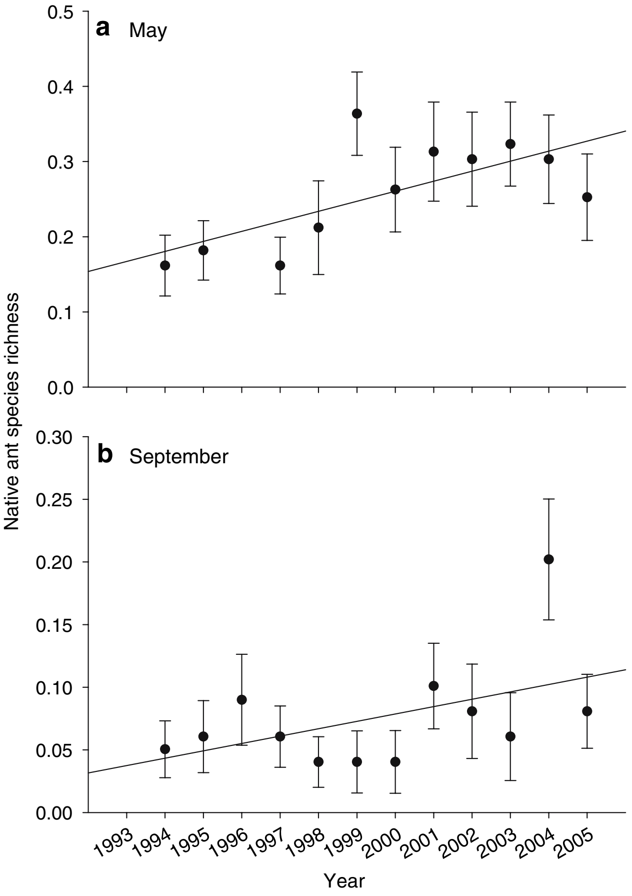

Fig. 5 Native ant species richness (mean ± SE) in invaded sample plots in May (**a**) and September (**b**) as a function of time since the survey began in 1993.Ninety-five sample plots invaded since 1993 are included in the calculation of the mean. *Line* is best-fit regression

aggregations. Our survey began after a 5-year drought (1987–1992) during which only 55% of average rainfall fell. The increase in rainfall in 1993 may have promoted Argentine ant survival and population growth, leading to the rapid range expansion seen in both May and September in the early years of the survey (Fig. 3). In later years, range expansion was observed only in the September surveys, perhaps due only to summer nest dispersal without the establishment of new winter aggregations.

When the survey began in 1993, the range of Argentine ants in JRBP was expanding in lower elevation grasslands and woodlands, near permanent water sources and human infrastructure (Human et al. 1998). The current invasion edge occurs at transitions to drier habitat, such as chaparral and high elevation grasslands and woodlands. *Linepithema humile* may have recently approached its maximum distribution in JRBP, due to abiotic constraints. If so, few new sites will be invaded in coming years, except in years of high rainfall. When another severe drought occurs, we anticipate a rapid range reduction.

Our results are consistent with those from other studies, mostly in plants, showing that fluctuations in resource availability influence the establishment and population growth of invasive species (Tilman 1999; Davis et al. 2000; Shea and Chesson 2002). An invasive annual grass species, *Bromus mollis*, invaded native-dominated serpentine grassland patches in JRBP in the wet El Niño years of 1982–1984 but was virtually eliminated in the drier years that followed (Hobbs and Mooney 1991). Other studies report that populations of invasive plants, birds, and insects became established in response to altered resource conditions during strong El Niño events (Rosenberg et al. 1990; Burgess et al. 1991; Roque-Albelo and Causton 1999; Dech and Nosko 2004).

The distribution of *L. humile* at JRBP increased rapidly during the summer following the very wet year associated with the 1997–1998 El Niño event (Fig. 2), and it showed more modest increases in other above-average rainfall years or in years with above-average summer rainfall. Since there is little evidence that native ant species richness affects Argentine ant invasion success in California (Erickson 1972; Holway 1998; Holway et al. 2002b; Sanders et al. 2003; Menke and Holway 2006), it appears that Argentine ant populations are primarily limited by soil moisture availability. Workers are small-bodied and desiccate easily (Tremper 1976; Walters and Mackay 2003). They move frequently to find high humidity nest sites (Heller and Gordon 2006) and in response to changes in weather (Gordon et al. 2001). Survival, reproductive rates, rate of spread, and abundance are higher in sites with high soil moisture (Holway et al. 2002b; Menke and Holway 2006). In a site near JRBP, DiGirolamo and Fox (2006) found that the abundance of *L. humile* in pitfall traps was significantly greater in 1998 following the high rainfall El Niño event than in 1999, 2000 and 2001. At JRBP, nest density (nest surface area × number of nests, m^{-2}) was up to fivefold higher at the invasion edge and twofold higher in the core of the invasion following the wet winter in 2002–2003 relative to the drier winter of 2001–2002 (Heller 2005). We cannot rule out alternative explanations for this increase in nest density between years, but it does suggest that in high rainfall years, nest site availability increases, as does Argentine ant abundance.

Two previous studies that examined the relationship between the spread of *L. humile* and rainfall – one in Hawaii over a 11-month period (Krushelnycky et al. 2004) and one in northern California over 4 years (DiGirolamo and Fox 2006) – did not find significant effects. The effect of rainfall on spread may become apparent only in a long-term study. For example, at JRBP, rainfall would not appear to be a significant predictor of spread if we examined any of the four-year increments in our 13-year study. Experimental manipulations of soil moisture, however, indicate that it can be important in the short term (Menke and Holway 2006).

Our results do not support our prediction that rainfall would increase the impact of *L. humile* on native ant species. Native ant species richness in invaded plots was not strongly related to rainfall, and two of the three native species we examined increased in high rainfall years in *Invaded* plots, and not in *Intact* plots. The response of each native species to rainfall probably depends on its life history. We found *P. imparis* in more sample plots in May following wet summers in the previous year, perhaps because rainfall in one year promoted dispersal or successful colony reproduction the following year. By contrast, the distribution of *F. moki* increased in September following wet summers in the same year, suggesting that rainfall promotes a short-term increase in foraging activity or colony size. Other studies show that abiotic conditions affect the activity of other native ant species in California (e.g., Holway et al. 2002b for *Forelius mccooki*). Our result that rainfall affects native ant distribution only in *Invaded* plots may not be due to any direct effect of rainfall on the interactions of native species with *L. humile*. In areas where *L. humile* is established, the structure of ant communities is disrupted (Sanders et al. 2003), and in these conditions, some native species may be able to benefit from increased rainfall.

Native ant species richness in invaded plots increased with time since the survey began (Fig. 5). In the early years of the survey, fewer native ant species co-occurred with *L. humile* than in later years. The impact of invasive ant species on native communities is often greatest immediately after the invasive species becomes established (Haskins and Haskins 1965; Crowell 1968; Lieberberg et al. 1975; Haskins and Haskins 1988; Morrison 2002; Sanders et al. 2003). For example, Morrison (2002) found that native ant species richness had reached pre-invasion levels 12 years after the invasion of a reserve in Texas by *Solenopsis invicta*, perhaps because the abundance of *S. invicta* decreased. We found a smaller increase in native ant species richness over 13 years than did Morrison (2002). We know little about changes in the abundance of Argentine ants at JRBP, but available evidence suggests they are increasing in abundance, rather than decreasing (Heller 2005). Most invaded sample plots at JRBP continued to be dominated exclusively by Argentine ants; the average proportion of invaded plots, over 13 years, that had only *L. humile* was 83 ± 10%. Thus, the slight rebound of the native ant community following invasion occurred in some – but not in most – of the sample plots.

Forecasting the effects of climate change on the distribution and dominance of invasive species is an important and complex task (Dukes and Mooney 1999; Mooney and Hobbs 2005). There are few long-term studies that link invasive species ecology to climate variability (Stachowicz et al. 2002). In California, regional climate models suggest that increases in temperature that result from greenhouse gas emissions may be accompanied by a decrease in both winter and summer precipitation (Kueppers et al. 2005), but predictions for precipitation are uncertain (Hayhoe et al. 2004). Global climate models predict that within the Pacific climate system there will be more years of climatic extremes and more extreme year-to-year variation in rainfall (Timmermann et al. 1999; IPCC 2007). Our results suggest that an increase in rainfall will increase the rate of spread of *L. humile* into new areas. If high rainfall years tend to alternate with dry years, it is likely that its distribution will expand and contract.

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