Population stability of a tree-galling aphid, *Baizongia pistaciae*, at three spatial scales

Robert J. Lamb,[1] Patricia A. MacKay, D. Wool

Abstract—The population stability of *Baizongia pistaciae* (Linnaeus) (Hemiptera: Aphididae) on its primary host, the tree *Pistacia palaestina* Boissier (Anachardiaceae), was investigated using 17–20 years of data from a study of gall abundance on individual trees in Israel. Abundance varied by at least an order of magnitude among adjacent trees, among locations, and among years. Stability was quantified for the alternate-year cohorts as population variability (PV) and persistence, at three spatial scales. PV (a proportion between 0 and 1) was similar between cohorts and declined with population scale – subpopulation (a tree): 0.676 ± 0.092 (± 1 SD, $n = 40$); population: 0.581 ± 0.098 (± 1 SD, $n = 6$); region: 0.424 (0.345 and 0.503, $n = 2$). Persistence (proportion of years that galls were present) was usually near 0.9, but 0.1 for some subpopulations, and 1.0 at the population and regional scales. Although protected within large galls on long-lived trees, the PV of *B. pistaciae* was similar to that of native, free-living aphid species on more ephemeral herbaceous hosts, but lower than for introduced aphid species. Persistence of *B. pistaciae* decreased as abundance decreased but not as PV increased. PV did not increase with the length of the study period; and declined with increasing population scale, because abundance was not synchronised among subpopulations or populations. PV was similar among populations, suggesting this parameter is characteristic of the species, although positive correlations between cohorts on a tree showed that PV was affected by the site-specific tree–grass habitats in which this species lives.

Résumé—Nous avons examiné la stabilité de la population de *Baizongia pistaciae* (Linnaeus) (Hemiptera: Aphididae) sur son hôte primaire *Pistacia palaestina* Boissier (Anachardiaceae) à l'aide d'une série de 17–20 ans de données provenant d'une étude de l'abondance des galles sur des arbres individuels en Israël. L'abondance varie par au moins un facteur de 10 entre les arbres adjacents, les sites et les années. Nous avons mesuré la stabilité des cohortes à tous les deux ans en termes de variabilité et de persistance de la population, à trois échelles spatiales. La variabilité de la population (PV, une proportion entre 0 et 1) est semblable entre les cohortes et diminue en fonction de l'échelle de la population – sous-population (un arbre): $0{,}676 \pm 0{,}092$ ($\pm ET$, $n = 40$); population: $0{,}581 \pm 0{,}098$ ($\pm ET$, $n = 6$), région: 0,424 (0,345 et 0,503, $n = 2$). La persistance (proportion des années pendant lesquelles les galles sont présentes) est généralement près de 0,9, mais elle est de 0,1 dans certaines sous-populations et de 1,0 aux échelles de la population et de la région. Malgré la protection offerte par les galles de grande taille sur des arbres à vie longue, *B. pistachiae* a PV semblable à celles d'espèces de pucerons indigènes à vie libre sur des plantes hôtes herbacées plus éphémères, mais inférieure à celle des espèces de pucerons introduites. La persistance de *B. pistaciae* décroît en même temps que l'abondance, mais non lorsque PV augmente. La variabilité de la population n'augmente pas en fonction de la durée de l'étude; elle décline lorsque l'échelle de la population augmente, parce que l'abondance n'est pas synchrone entre les sous-populations ni les populations. PV est semblable entre les populations, ce qui laisse croire que ce paramètre est une caractéristique de l'espèce, bien que des corrélations positives entre les cohortes sur un même arbre montrent que PV est affectée par les habitats d'arbres et d'herbes spécifiques aux sites dans lesquels vit cette espèce.

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Introduction

The stability of a population is a complex phenomenon, requiring at least two parameters, population variability and persistence, to encompass the concept (Grimm and Wissel 1997; Lamb and MacKay 2010; Lamb *et al.* 2011). Population variability reflects the ups and downs in abundance of a population from year to year, estimated here by PV, a proportion between 0 and 1 (Heath 2006). A species that fluctuates widely in abundance has a high PV, and is perceived to be less stable than one that fluctuates less widely. A species that frequently disappears from a habitat also is perceived to have a less stable population than one that is more persistent, even if both fluctuate similarly. Persistence is defined here as the probability that a species occurs in a particular year at a location, estimated as the proportion of years in a time series of annual abundance that the species is present (Lamb and MacKay 2010).

The stability of relatively few insect populations has been quantified using these metrics, because long time series of population abundance are required, and because robust methods to quantify the parameters, particularly population variability, have only recently been developed. The eight populations of four species of aphids (Hemiptera: Aphididae) for which stability has been quantified have high PV and high persistence (Lamb and MacKay 2010; Lamb *et al.* 2011). These species are free-living herbivores of herbaceous plants, representing some, but by no means all of the variation in life history exhibited by aphid populations.

Three populations of the aphid *Baizongia pistaciae* (Linnaeus) were sampled in Israel for 20 years on its primary host, the tree *Pistacia palaestina* Boissier (Anachardiaceae), to diagnose underlying causes of temporal changes in abundance (Wool 2002). Only weak correlations with weather and "no convincing evidence of self regulation (density dependence)" were detected (Wool 2002). Wool's (2002) study provides time series of abundance that are used here to assess the stability of populations of an aphid with a more permanent host than, and a life history that differs from, the aphids so far investigated. *Baizongia pistaciae* has a 2-year life cycle, alternating between a primary host tree and a secondary host, a grass (Graminae) (Wool 1990, 2002, 2004). The aphid passes through three generations in one summer within characteristic large galls on *Pistacia*. As summer ends, winged females migrate to the soil and produce larvae that are free-living and feed on the roots of a grass. Their offspring and subsequent asexual generations continue feeding on grass roots through the winter and following summer before migrating back to *Pistacia* the next autumn. These asexual migrants produce a single sexual generation on *Pistacia*. A sexual female lays a single egg that overwinters and the parthenogenetic female larva that hatches the following spring initiates a gall. This 2-year life history results in two cohorts that form galls on the trees in alternate years. The cohorts probably have little opportunity to mix, but the extent of genetic exchange between cohorts is not known.

Pistacia trees can be long-lived and often grow in close proximity to the secondary grass host (Martinez *et al.* 2005). Therefore, this tree–grass system is a more permanent habitat at a particular location than many herbaceous plants, particularly crops. We expected the longevity of its primary host would stabilise populations of *B. pistaciae*. We also expected the galling habit of *B. pistaciae* would stabilise populations by protecting them from fluctuating levels of predation and extremes of weather (Wool 2002; Martinez *et al.* 2005), more so than is the case for free-living aphids feeding on herbaceous foliage during summer. Furthermore, we expected populations of *B. pistaciae*, a native aphid, to be more stable than those of introduced aphids (Lamb *et al.* 2011). The annual abundances of galls (Wool 2002) are used here to estimate the stability of *B. pistaciae* and compare its stability with that of free-living native and introduced aphids on herbaceous plants (Lamb and MacKay 2010; Lamb *et al.* 2011).

The data on the abundance of *B. pistaciae* (Wool 2002) were collected for two cohorts, from three populations of marked trees, and over many sexual cycles, which provides replication within subpopulations (the local habitat), among subpopulations (individual trees), and among populations. This replication allowed us also to examine hypotheses proposed previously to explain population stability, hypotheses that are more general than those related to the specific life history traits of *B. pistaciae*, as follows: stability is a function of average population abundance, particularly that low abundance contributes to low persistence (Schoener and Spiller 1987) and

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persistence declines as population variability increases (Inchausti and Halley 2003); more time leads to more population variability (Lawton 1988; Pimm and Redfearn 1988; Inchausti and Halley 2002); stability increases with spatial scale (Connell and Sousa 1983); stability is a species trait (Taylor and Woiwod 1980; Lamb and MacKay 2010; Lamb *et al.* 2011).

Materials and methods

The annual abundance of *B. pistaciae* was estimated by counting galls on individual marked trees each winter at three locations from 1979 to 1998 (Wool 2002). The galls are large, long-lasting, and easily counted when trees shed their leaves. Trees were sampled at Mount Carmel in the north of Israel (seven trees for 20 years), at Beit Guvrin in the southeast (six trees for 19 years), and at Tel Aviv in the southwest (24 trees for 17 years); site names are abbreviated to Carmel, Guvrin, and Tel Aviv and used to identify aphid populations. Other trees sampled for shorter periods were excluded from this study to allow consistent comparisons over similar time intervals. The temporal changes in abundance of the aphid, and the characteristics and precise locations of the populations are described by Wool (2002) and references therein.

The galls on a tree were considered to belong to even-year and odd-year cohorts, because of the 2-year life cycle of the aphid. The cohorts were analysed separately, providing time series of 8–10 cycles over the 17–20 years, and replicate subpopulations on individual trees to assess the effect of local habitat on abundance and stability. The three population scales were: subpopulation, the galls on an individual tree ("patch" in Wool 2002); population, a group of trees at one location; and region, pooled data for three populations. For *B. pistaciae*, dispersal of more than 100 m between local tree–grass habitats is limited and longer-distance dispersal between locations is less likely, justifying the conclusion that an individual tree and surrounding grass is "the smallest area in the landscape that sustains a genetically differentiated subpopulation" (Martinez *et al.* 2005). The estimates of abundance each year for the three spatial scales were calculated as follows: subpopulation – the number of galls on an individual tree; population – the total number of galls on sampled trees at a location divided by the number of trees; region – the average of the three population-scale estimates, which assured that each population estimate contributed equally to the regional estimate although the number of trees sampled differed among populations.

Three population parameters were considered: abundance, population variability, and persistence. Abundance was estimated as described above. Population variability was estimated by the metric PV, the average of the differences for all pairs of abundance in a time series, with each difference divided by the larger abundance of the pair, assuring the index is a proportion between 0 and 1 (Heath 2006). Persistence was estimated as the proportion of 2-year cycles in which galls were present: for example, if galls of the even-year cohort were found in 9 of 10 years, persistence was 0.9.

Sources of variation in abundance were analysed by two-way and three-way analyses of variance on ln-transformed or square-root-transformed data to assure normality (SYSTAT 2009). The variance in abundance (and related estimates of variability) estimated from year-to-year fluctuations, which assumes annual abundance is normally distributed and independent from year to year, was not considered to be a valid estimate of population variability (Heath 2006; Lamb and MacKay 2010; Lamb *et al.* 2011). Population variability was assumed to be normally distributed because each PV is a mean of many differences (Heath 2006). PV was analysed as for abundance, but without transformation. Persistence values were proportions based on relatively small samples ($n = 8$–10 years) and were between 0.8 and 1.0 for many subpopulations. Therefore, persistence was not subject to analysis of variance. Relationships between population parameters were assessed using Pearson product-moment correlation or linear regression (SYSTAT 2009). Correlation analyses also were used to assess the similarity of population parameters between the cohorts inhabiting trees in alternate years.

Results

Variation in gall abundance

On individual trees, galls were most abundant at Guvrin, with a mean of 64 galls per tree, compared with 43 at Carmel, and five at Tel Aviv (Table 1). The difference between Carmel and Guvrin was detected in analysis of variance

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Table 1. Population parameters and standard deviations (±1 SD, n = the number of trees) of *Baizongia pistaciae* galls on individual *Pistacia* trees (subpopulation scale) from the even-year and odd-year cohorts of a 2-year life cycle at three locations in Israel.

	Location							
	Carmel (7 trees)		Guvrin (6 trees)		Tel Aviv (24 trees)		Tel Aviv (7 trees)*	
Cohort	Galls/tree	Years	Galls/tree	Years	Galls/tree	Years	Galls/tree	Years
Abundance								
Even	37.9 ± 39.9	10	63.9 ± 43.0	8 or 9	2.2 ± 2.8	8	5.6 ± 2.8	8
Odd	47.8 ± 36.1	10	64.8 ± 61.1	10	7.1 ± 5.3	9	19.2 ± 14.7	9
PV								
Even	0.705 ± 0.089	10	0.690 ± 0.082	8 or 9	0.501 ± 0.235	8	0.716 ± 0.047	8
Odd	0.596 ± 0.111	10	0.710 ± 0.047	10	0.566 ± 0.199	9	0.672 ± 0.085	9
Persistence								
Even	0.886 ± 0.107	10	0.942 ± 0.095	8 or 9	0.370 ± 0.237	8	0.625 ± 0.161	8
Odd	0.914 ± 0.186	10	0.917 ± 0.075	10	0.551 ± 0.292	9	0.873 ± 0.010	9

The parameters are: abundance, the mean number of galls on a tree over years; population variability estimated by PV (see "Materials and methods"); and persistence, the proportion of years galls were present on a tree.

*All subpopulations (trees) at Tel Aviv with persistence ≥0.5.

of ln-transformed gall abundance, with variance partitioned among locations, cohorts, years within cohorts, and subpopulations within location ($F = 5.2$, df = 1, 218, $P = 0.024$). At Tel Aviv, some trees were often free of galls, and the distribution was not normalised by ln-transformation. The difference between Tel Aviv and the other two locations was detected by analysis of variance of untransformed annual mean gall abundance for subpopulations at a location, using a General Linear Model which partitioned variance between the cohorts and among locations ($F = 10.2$, df = 2, 48, $P < 0.001$).

Gall abundance differed among subpopulations at each location, and between the even-year and odd-year cohorts at Carmel and Tel Aviv although not at Guvrin (Table 1). These differences confirmed the validity of treating the galls on different trees as distinct subpopulations, and considering even-year and odd-year cohorts separately. Differences in abundance among subpopulations and between cohorts were detected in two-way analyses of variance for each location, as follows: Carmel, ln-transformed data for subpopulations ($F = 8.4$, df = 6, 126, $P < 0.001$) and cohorts ($F = 4.6$, df = 1, 126, $P = 0.034$, nonsignificant interaction); Guvrin, ln-transformed data for subpopulations ($F = 3.9$, df = 5, 98, $P < 0.003$) but not cohorts ($F = 0.014$, df = 1, 98, $P = 0.906$, nonsignificant interaction); and Tel Aviv, square-root-transformed data for subpopulations ($F = 10.8$, df = 23, 336, $P < 0.001$) and cohorts ($F = 42.4$, df = 1, 336, $P < 0.001$, significant interaction).

Variation in population stability

Persistence was near 0.9 for both cohorts at Carmel and Guvrin, but low for most of the 24 subpopulations at Tel Aviv (Table 1). PV for subpopulations ranged from 0.50 to 0.71, on average, for the two cohorts and three populations, with PV lowest for both cohorts at Tel Aviv (Table 1). Analysis of variance of PV using a General Linear Model detected differences among locations ($F = 4.2$, df = 2, 68, $P = 0.020$), but not between cohorts within location ($F = 1.3$, df = 3, 68, $P = 0.299$). When the analysis was repeated excluding data from Tel Aviv where abundance was low, no difference in PV was detected between Carmel and Guvrin ($F = 0.83$, df = 1, 22, $P = 0.372$) or between cohorts within location ($F = 2.2$, df = 2, 22, $P = 0.135$).

All three population parameters for the 24 subpopulations at Tel Aviv differed from those at the other two locations and therefore variation among subpopulations was examined separately at the three locations. PV differed among subpopulations at Carmel and Guvrin but not at Tel Aviv, and PV was lower for the odd-year than the even-year cohort at Carmel, but

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Table 2. Pearson correlation coefficients, with probability that the coefficient = 0 in parentheses (*P*), comparing population parameters for 8–10 cycles of *Baizongia pistaciae* galls from the even-year and odd-year cohorts on individual *Pistacia* trees in Israel.

	Correlation coefficient (*P*)	
Parameter	Abundance	PV
Carmel and Guvrin, persistence ≥0.5 (13 trees, 2 cohorts, $n = 26$)		
PV	−0.354 (0.076)	–
Persistence	0.516 (0.007)	−0.374 (0.060)
Tel Aviv, persistence = 0–1 (24 trees, 2 cohorts, $n = 45$)*		
PV	0.412 (0.005)	–
Persistence	0.627 (<0.001)	0.784 (<0.001)
Tel Aviv, persistence <0.5 (15–16 trees, 2 cohorts, $n = 31$)*		
PV	0.652 (<0.001)	–
Persistence	0.589 (<0.001)	0.640 (<0.001)
Carmel, Guvrin and Tel Aviv, persistence ≥0.5 (20 trees, 2 cohorts, $n = 40$)		
PV	−0.298 (0.062)	–
Persistence	0.603 (<0.001)	−0.286 (0.073)

The parameters are: abundance, the mean number of galls on a tree over years; population variability estimated by PV (see "Materials and methods"); and persistence, the proportion of years galls were present on a tree. Estimates were made for: pooled data for subpopulations (trees) at Carmel and Guvrin with high abundance and persistence ≥0.5; at Tel Aviv with low abundance, first for all subpopulations; then for subpopulations with persistence <0.5; and then for subpopulations from three locations with persistence ≥0.5.

*A cohort on a tree with 0 galls in all years was excluded.

not at Guvrin or Tel Aviv (Table 1). These differences were detected in two-way analyses of variance, as follows: Carmel, for subpopulations ($F = 21.5$, df = 6, 6, $P = 0.001$) and cohorts ($F = 46.2$, df = 1, 6, $P < 0.001$); Guvrin, for subpopulations ($F = 10.0$, df = 5, 5, $P = 0.012$) and cohorts ($F = 0.02$, df = 1, 5, $P = 0.893$); and Tel Aviv for subpopulations ($F = 1.59$, df = 21, 21, $P = 0.149$) and cohorts ($F = 2.2$, df = 1, 21, $P = 0.152$).

Relationships among population parameters

Although the average abundance of galls on individual trees varied by as much as an order of magnitude among locations and also varied between the cohorts at two locations, PV was relatively uniform (Table 1). Mean persistence, however, tended to be high when gall abundance and PV were high (Table 1). These relationships were detected by estimating Pearson correlation coefficients: PV versus abundance ($R = 0.795$, $n = 6$, $P > 0.05$); persistence versus abundance ($R = 0.935$, $n = 6$, $P = 0.006$); persistence versus PV ($R = 0.864$, $n = 6$, $P = 0.026$).

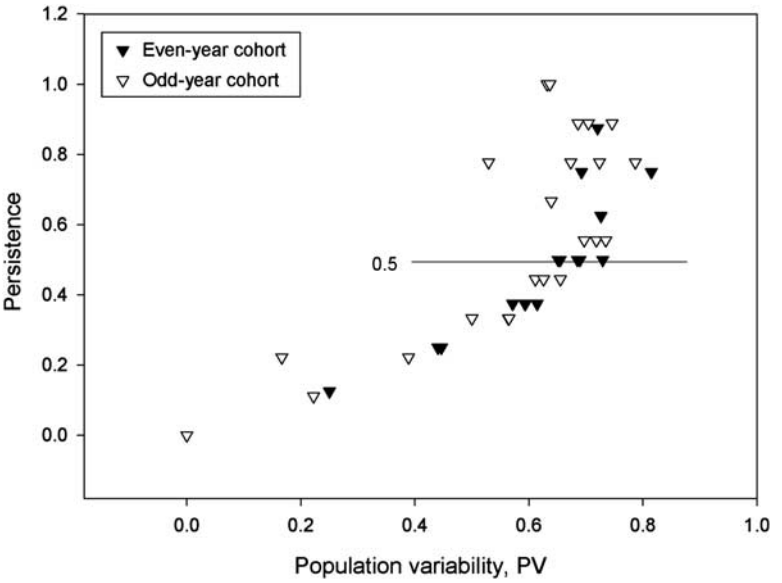
When the relationships among population parameters were examined for individual subpopulations instead of means for subpopulations at a location, more complex patterns emerged. For the 13 subpopulations at Carmel and Guvrin the relationships between gall abundance and PV and between PV and persistence were weak and negative (Table 2), contrary to the strong positive correlations for populations described above. The relationship between abundance and persistence remained positive (Table 2), as expected from the mean values (Table 1). For the 24 subpopulations at Tel Aviv, however, positive relationships were detected among all three parameters (Table 2).

The contrast between the relationships among population parameters at Carmel and Guvrin, on the one hand, and Tel Aviv, on the other, was clarified by considering the relationships between PV and persistence at Tel Aviv in detail (Fig. 1). Persistence increased with PV up to a persistence of 0.5 ($R = 0.640$, $n = 31$, $P < 0.001$; Pearson correlation), but not above 0.5 ($R = -0.092$, $n = 14$, $P = 0.754$). The relationship between PV and abundance at Tel Aviv also disappeared when persistence was ≥0.5 ($R = 0.207$, $n = 14$,

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Fig. 1. Relationship between persistence (proportion of years galls are present) and population variability (PV, defined in "Materials and methods") of *Baizongia pistaciae* galls, from even-year and odd-year cohorts, on 24 *Pistacia* trees at Tel Aviv, Israel.



$P = 0.478$). When only subpopulations with low gall persistence were considered at Tel Aviv, all relationships between population parameters were positive (Table 2). When only subpopulations with high persistence were considered from all three locations, two of the relationships were negative and weak, and the only significant relationship was between abundance and persistence (Table 2). When half or more of the estimates of abundance in a time series were 0, PV and persistence decreased in proportion to the increased number of 0-values, assuring positive correlations among them. We conclude these positive correlations for low-persistence subpopulations were a numerical consequence of the large number of 0-values that occurred when persistence was near 0.1, rather than meaningful ecological relationships.

Considering low and high persistence cohorts at Tel Aviv separately, and pooling the high persistence cohorts at Tel Aviv with the cohorts from Carmel and Guvrin, the positive relationship between abundance and persistence was evident, and this relationship was nonlinear (Fig. 2A). The relationship was, however, approximately linear and positive when mean annual abundance was >10 galls per tree ($R = 0.918$, $n = 5$, $P = 0.028$; Pearson correlation). The one cohort from Tel Aviv with gall abundance above a threshold of about 10 galls per tree had a persistence consistent with the data from Carmel and Guvrin (Fig. 2A). The persistence of galls on the other trees at Tel Aviv, with abundance <10, declined sharply as abundance declined (Fig. 2A).

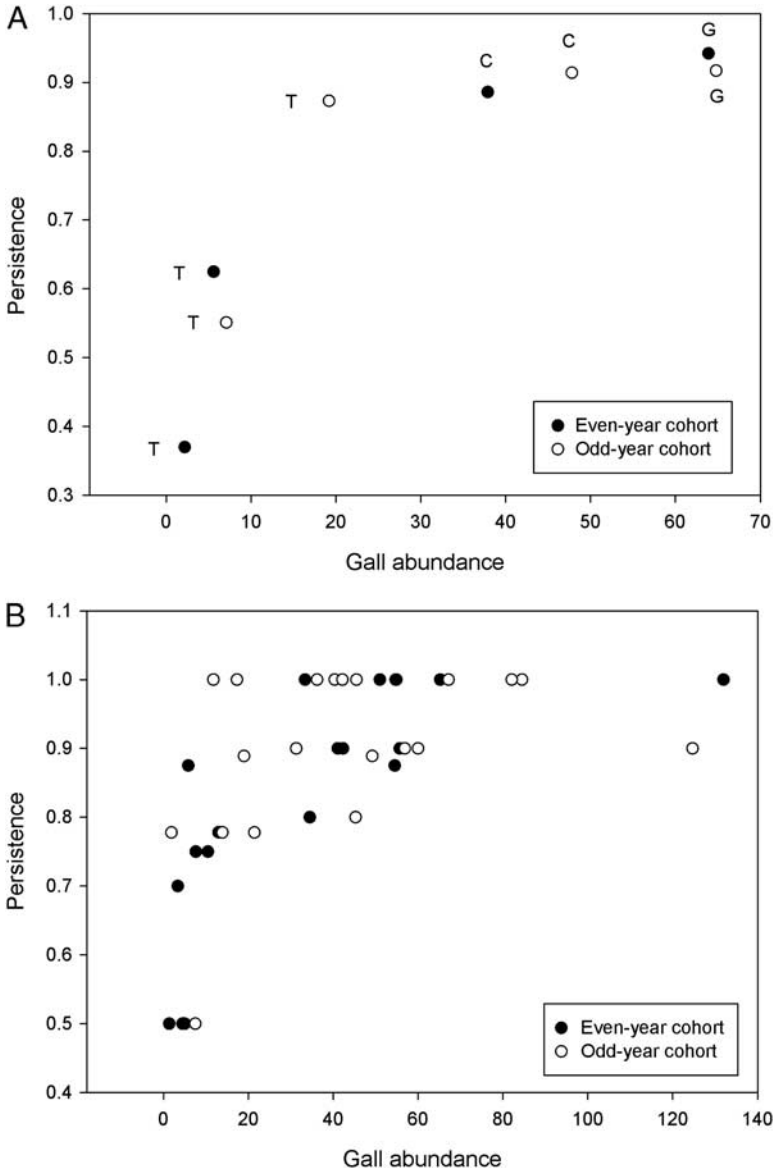
Population parameters for subpopulations with high persistence

To eliminate any numerical anomaly resulting from many 0-values, population parameters were re-estimated for the 20 subpopulations with high persistence: seven at Carmel; six at Guvrin; and seven at Tel Aviv. Persistence was 0.63 for one cohort at Tel Aviv, but otherwise 0.87–0.94 (Table 1). Gall abundance differed by up to 10 times among populations and also differed between cohorts (Table 1). The differences were detected in a mixed model analysis of variance: for populations ($F = 7.9$, df = 2, 17, $P = 0.004$) and cohorts ($F = 8.5$, df = 1, 19, $P = 0.009$). For these subpopulations, PV for one cohort at Carmel was 0.60, but otherwise was 0.67–0.72 (Table 1). No difference in PV was detected in a two-way analysis of variance with a nonsignificant interaction, neither among populations ($F = 0.87$, df = 2, 34, $P = 0.43$) nor

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Fig. 2. Relationships between persistence (proportion of years galls are present) and abundance (number of galls averaged over the time series) of *Baizongia pistaciae* galls, from even-year and odd-year cohorts, on *Pistacia* trees in Israel: A. Mean values for subpopulations at Carmel (C) and Guvrin (G), and for low-persistence (<0.5) and high-persistence (≥ 0.5) subpopulations at Tel Aviv (T); B. Estimates for 20 individual subpopulations and two cohorts from three populations, with persistence ≥ 0.5.



between cohorts ($F = 3.22$, df = 1, 34, $P = 0.08$). For the region, the mean PV for *B. pistaciae* galls on individual trees with persistence ≥ 0.5 was 0.676 ± 0.015 (SE, $n = 40$).

For the 20 frequently colonised trees, the relationship between persistence and abundance was positive, with the lowest persistence occurring when a tree had fewer than 10 galls (Fig. 2B). Persistence increased with abundance (linear regression coefficient = 0.003, $F = 21.7$, df = 1, 38, $P < 0.001$). No relationship was detected between abundance and PV (linear regression coefficient = -0.001, $F = 3.7$, df = 1, 38, $P = 0.061$) or between PV and persistence (linear regression

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coefficient = −0.509, $F = 3.4$, df = 1, 38, $P = 0.073$), although in the latter case the regression coefficient was relatively large with $P < 0.1$, and negative as expected if persistence increases with PV.

Population stability and sampling interval

PV showed no consistent pattern with the length of the sampling interval for any of the locations (Table 3). For the "more-time–more-variation" hypothesis to be supported, regression coefficients would need to be consistently and significantly positive, which they were not. PV was regressed against the number of sexual generations for each cohort and subpopulation, as the length of the time series increased. The first two estimates of PV from the first three cycles in each time series were excluded because variation in PV was high as expected when only two to three sexual generations contributed to the estimate (Lamb and MacKay 2010).

Population stability and spatial scale

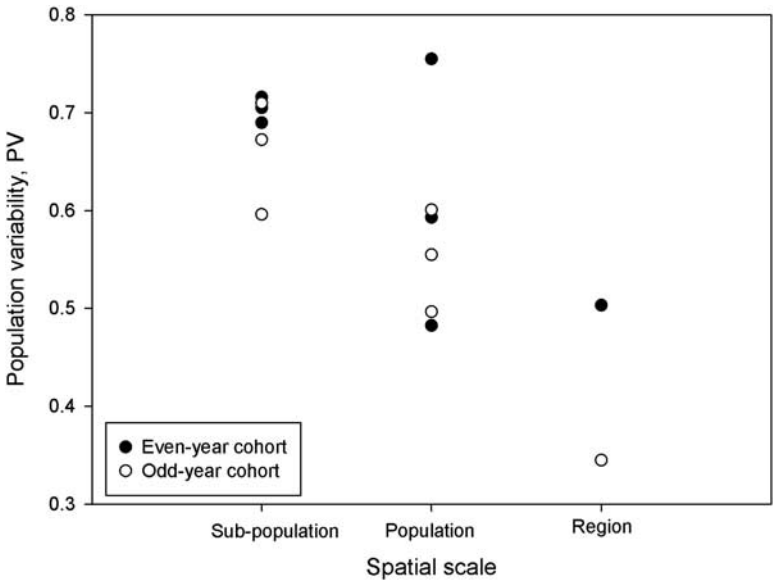
PV for *B. pistaciae* declined as the spatial scale increased, based on the 20 trees where galls were usually present (Fig. 3). For clarity, the plotted points at the subpopulation scale are the means from Table 1, rather than the 40 values for individual trees. At the population scale, the highest value is for Tel Aviv and the two lowest values are

Table 3. Frequency of positive (+) and negative (−) linear regression coefficients relating population variation (estimated by PV) in a time series to the length of the time series for individual subpopulations and cohorts.

Location (df)	+, $P < 0.05$*	−, $P < 0.05$	+, $P > 0.05$	−, $P > 0.05$
Carmel (1, 6)	2	2	7	3
Guvrin (1, 5 or 6)	2	4	4	2
Tel Aviv (1, 6)	3	0	2	9

A more-time–more-variation effect predicts a positive coefficient.
*Probability that the coefficient differs from 0.

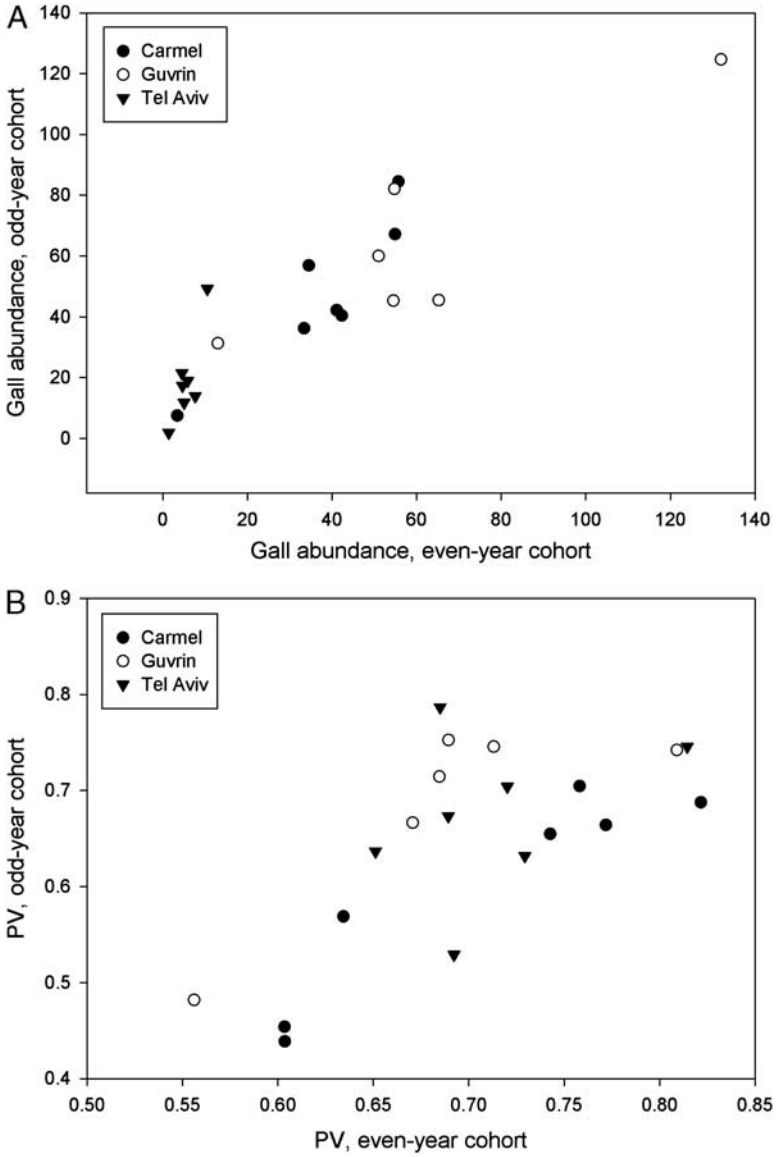
Fig. 3. Population variability (PV, defined in "Materials and methods") of *Baizongia pistaciae* galls, from even-year and odd-year cohorts, on *Pistacia* trees at three spatial scales in Israel. For clarity, mean values for subpopulations (trees) at each location and for each cohort are plotted instead of the 40 individual estimates.



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Fig. 4. Relationships between even-year and odd-year cohorts of *Baizongia pistaciae* for gall abundance (average number of galls over time) (A); and population variability (PV, defined in "Materials and methods") (B), for 20 subpopulations with high persistence (≥ 0.5) on individual *Pistacia* trees, from three populations in Israel.



for Carmel and Guvrin (Fig. 3). Mean values for PV at the three spatial scales were as follows: subpopulation – 0.704 ± 0.013 (± 1 SD, $n = 20$) and 0.659 ± 0.058 (± 1 SD, $n = 20$); population – 0.610 ± 0.137 (± 1 SD, $n = 3$) and 0.551 ± 0.052 (± 1 SD, $n = 3$); region – 0.503 ($n = 1$) and 0.345 ($n = 1$), for even-year and odd-year cohorts, respectively. A one-way analysis of variance detected a reduction in PV from subpopulation ($n = 40$) to population ($n = 6$) scale ($F = 5.51$, df = 1, 44, $P = 0.024$). PV declined by about 15% from subpopulation to population and by 17% or more from population to regional scale.

The decline in PV from subpopulation to population was associated with low correlations among the annual gall abundance for many of the subpopulations. At each of the three locations (6 or 7 subpopulations), one-third of the

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Table 4. Pearson correlation coefficients, followed by the probability that the coefficient = 0 in parentheses, between the even-year and odd-year cohorts of *Baizongia pistaciae* galls on *Pistacia* trees at three locations in Israel, for three population parameters (abundance, population variability, and persistence) estimated for individual subpopulations (trees).

Location	Abundance	PV	Persistence
Carmel (7 trees)	0.900 (0.006)	0.933 (0.002)	0.848 (0.016)
Guvrin (6 trees)	0.885 (0.019)	0.842 (0.035)	0.513 (>0.05)
Tel Aviv (7 trees)	0.851 (0.015)	0.340 (>0.05)	−0.143 (>0.05)

PV quantifies population variability.

57 possible Pearson correlation coefficients (all positive) comparing year-to-year gall abundance between pairs of subpopulations were significant ($n = 17$–20 years, $P < 0.05$). The decline in PV from population scale to regional scale also was associated with low correlations among the annual mean gall abundance for the three populations (Pearson correlation coefficients = 0.041, −0.089, −0.319; $n = 16$ years, $P > 0.229$). Synchronisation in abundance from year to year was weak between individual subpopulations within a population and absent between populations.

The persistence of *B. pistaciae* was relatively low at the subpopulation scale, particularly at Tel Aviv where many of the 24 trees were without galls in particular years (Table 1). At the population scale, however, galls were present every year in all three populations, although at Tel Aviv in 1988 only one gall was present on one of the 24 trees. With a persistence of one at the population scale, persistence was also one at the regional scale.

Habitat specificity of population parameters

The even-year and odd-year cohorts had consistently low, intermediate, or high gall abundance on individual trees over the 8–10 cycles (Fig. 4A). PV was also characteristic of the subpopulation on an individual tree, with both cohorts having relatively low PV on some trees, and relatively high PV on other trees (Fig. 4B). For 20 subpopulations and two cohorts, PV ranged from 0.44 to 0.82. Considering individual subpopulations, gall abundance was positively correlated between cohorts in each population, PV was positively correlated between cohorts at Carmel and Guvrin, and even persistence with a narrow range of values was positively and highly correlated between cohorts at Carmel (Table 4). The consistency between cohorts was evident from the following examples: at Carmel, Tree 5 had three and eight galls, on average, whereas Tree 9 had 56 and 85 galls for the two cohorts; at Guvrin, Tree 16 had 13 and 31 galls, on average, whereas Tree 14 had 132 and 125 for the two cohorts; at Tel Aviv, Tree 18 had one and two galls, on average, whereas Tree 14 had 11 and 49 for the two cohorts. The trees with lowest and highest gall abundance in each population usually differed by an order of magnitude, for both cohorts. Similar patterns of difference in PV were observed. Nevertheless, no relationship was detected between abundance and PV; individual subpopulations with similar gall abundance did not necessarily have similar PV (Table 2).

Discussion

Three populations of *B. pistaciae* persisted throughout the 17–20-year study, and so were in that sense stable. PV, however, was relatively high: PV was 0.581 ± 0.040 (SE) with a range of 0.483–0.755 ($n = 6$). This level of PV is similar to that of two other native aphids, *Uroleucon rudbeckiae* (Fitch) with PV = 0.648 ± 0.036 (SE) (Lamb and MacKay 2010) and *Macrosiphum euphorbiae* (Thomas) with PV = 0.585 (Lamb *et al.* 2011). Thus, the more permanent tree–grass habitat and galling habit of *B. pistaciae* did not stabilise its populations as expected, when compared with free-living native aphid species on herbaceous foliage. Although the primary host of *B. pistaciae* is a long-lived tree, the secondary host is a grass (Wool 2004). Temporal variation in the proximity of alternate hosts (Martinez *et al.* 2005) or other aspects of the complex interaction between alternate hosts may destabilise populations of *B. pistaciae*. If host-alternation is indeed destabilising, the population dynamics of aphid

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species that use only trees as hosts would be expected to have lower PV than *B. pistaciae*.

Lamb *et al.* (2011) note that two native species of aphids have lower PV than two introduced species. The PV of the native *B. pistaciae* also is lower than that of two introduced aphid species, *Myzus persicae* (Sulzer) (PV = 0.771) and *Aphis nasturtii* (Kaltenbach) (PV = 0.831) (Lamb *et al.* 2011), consistent with other native species. More examples of native and introduced aphid species are required to confirm this generality.

Parameters that define the population dynamics of species are thought to be interrelated, reflecting the density-dependent processes that underlie them (Taylor and Woiwod 1980). For example, low population persistence is hypothesised to be a consequence of high population variability (Inchausti and Halley 2003). For *B. pistaciae*, however, no consistent relationship was detected between persistence and population variability. The trend of persistence with PV for subpopulations with persistence ≥ 0.5 was negative, as expected, but not significant. For trees with persistence <0.5, persistence increased with PV, contrary to expectations, probably because of the numerical relationships among parameters when a time series has many 0-values for abundance. At the population scale, low and high persistence populations had essentially the same PV. However, persistence of *B. pistaciae* was associated with abundance: persistence was low when average abundance was low. Reduced persistence is also more closely associated with low abundance than high population variability for four other species of aphid (Lamb and MacKay 2010; Lamb *et al.* 2011) and for some spiders (Schoener and Spiller 1987). PV, however, was unrelated to abundance at the subpopulation or population scale. The independence of persistence and PV, and the difference in the relationships between persistence and abundance in comparison with PV and abundance support the idea that persistence and population variability are distinct components of stability, determined by different aspects of the population dynamics of a species.

Population variability has been hypothesised to increase with time, the more-time–more-variation effect (Lawton 1988; Pimm and Redfearn 1988; Inchausti and Halley 2002). No consistent increase in PV was detected for *B. pistaciae*, however. A similar lack of increase in variation with time was observed in populations of four other aphid species (Lamb and MacKay 2010; Lamb *et al.* 2011). The 17–20 years, 8–10 iterations of the 2-year life cycle, represents a long study in practical terms, but may be too short to detect a more-time–more-variation effect.

Population variability of the two cohorts of *B. pistaciae* declined as the scale of the study increased. A decline is expected if differences in year-to-year fluctuations for different subpopulations or populations average out because they are asynchronous (Connell and Sousa 1983). Indeed, few correlations between annual abundance were detected between subpopulations even when trees were relatively near to each other, and none were detected between populations of *B. pistaciae*. The fluctuations of these populations are independent of and therefore not synchronised by weather (Wool 2002). In contrast, subpopulations and populations of *U. rudbeckiae* are highly synchronised and show no decline in population variability as spatial scale increases (Lamb and MacKay 2010). Population variability declines with scale but probably only when populations do not fluctuate in synchrony.

The contrast in the effect of spatial scale on population variability between *B. pistaciae* and *U. rudbeckiae* suggests that interspecific comparisons need to be made between equivalent scales. A subpopulation of *B. pistaciae* includes the galls on an individual tree, whereas a subpopulation of *U. rudbeckiae* includes the colonies on a group of stems in a patch of plants. The mean number of galls per tree varied from 2 to 65, on average, numerically similar to the number of *U. rudbeckiae* colonies in a patch of host plants (Lamb and MacKay 2010). A population of *B. pistaciae* consists of the galls on a group of adjacent trees along a few kilometres of road, whereas a population of *U. rudbeckiae* consists of the colonies on a group of plant patches along 1–3 km of trail (Lamb and MacKay 2010). For these two aphid species, the spatial scales relative to the sampling scale and the abundance of aphids in the sampling units are equivalent. However, where spatial scales are not ecologically equivalent, interspecific comparisons are questionable: for example, for comparisons between species with different dispersal capacities or from habitats with different spatial characteristics.

PV is often considered to be a species characteristic (Taylor and Woiwod 1980). For the few aphid species studied, species-specificity is

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supported either because PV is uniform among spatial scales and populations for *U. rudbeckiae* (Lamb and MacKay 2010), or because PV is consistently different among species from decade to decade for three potato-colonising aphid species living in the same habitat (Lamb *et al.* 2011). At the subpopulation spatial scale, *B. pistaciae* also shows similar PV, on average, among populations and between cohorts. However, PV at the population scale, ranging from 0.48 to 0.76, is less uniform than might be expected if it is primarily a species trait. Perhaps more importantly, subpopulations on individual trees show characteristic abundances and PV, based on the correlation between cohorts for each of these two parameters. At the subpopulation scale, the population variability of *B. pistaciae* depends at least in part on characteristics of the habitat it finds itself in, the specific tree and associated secondary host grass. Furthermore, the aphid itself is an important factor in shaping the quality of its habitat through its effect on the architecture of its primary host. Kurzfeld-Zexer *et al.* (2010) find that infestation of *Pistacia* trees by *B. pistaciae* early in a tree's life changes its growth form from tree shape to multi-stemmed shrub shape, and the shrubby form is more susceptible to subsequent infestation by the aphid than the tree form. Thus, at the subpopulation scale, population variability results from the interaction of the aphid with its habitat. Nevertheless, differences in PV among subpopulations average out so that the mean PV for different populations is similar. The interaction between aphid and its tree–grass habitat must be similar, on average, for the three locations. This characteristic level of population variability is maintained in different populations even though genetic differentiation occurs among populations, which results from limited dispersal by the aphid (Martinez *et al.* 2005).

The unique abundance and stability properties of *B. pistacia* on individual trees might be due to the resistance level of the tree to the aphid, some site-specific or tree-specific habitat characteristic (*e.g.*, proximity to patches of the secondary grass host), or genetic differentiation of the aphids that use that tree (Martinez *et al.* 2005). The importance of individual trees or tree–grass units of habitat in determining the dynamics of the subpopulation is shown by the similar dynamics of the two genetically independent cohorts. Interestingly, population variability is not related to abundance, confirming that for *B. pistaciae*, as for the aphids studied previously (Lamb and MacKay 2010; Lamb *et al.* 2011), both parameters must be quantified to define the population dynamics of a species.

Baizongia pistaciae forms a large gall on its primary host, a *Pistacia* tree, and alternates with the roots of its secondary host, a grass, in a 2-year life history (Wool 2004). It interacts with individual long-lived host trees in a way that results in genetic differentiation at the subpopulation scale (Martinez *et al.* 2005). The aphid causes phenotypic changes in the host that alter the subsequent suitability of the host to the aphid (Kurzfeld-Zexer *et al.* 2010). In spite of the marked difference between this life history and that of native aphid species that feed as free-living herbivores on ephemeral herbaceous hosts (Lamb and MacKay 2010; Lamb *et al.* 2011), stability measured as population variability and persistence is remarkably similar for *B. pistaciae* and these other native aphids. Persistence of *B. pistaciae* decreases as average abundance decreases but is not related to population variability, and population variability does not increase with the length of the study. The same relationships have been observed for other aphid species (Lamb and MacKay 2010; Lamb *et al.* 2011). Unlike *U. rudbeckiae* (Lamb and MacKay 2010), the population variability of *B. pistaciae* declines with population scale, because abundance of the former species is synchronised among subpopulations and populations, whereas the population fluctuations of the latter species are not. The PV of *B. pistaciae*, like that of other aphid species, is relatively high, above 0.5 on a scale of 0–1, and clearly reflects an important trait of the population dynamics of the species, independent of average abundance.

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