



CHICAGO JOURNALS



Pest and Parasite Species-Richness Problems

Author(s): Andrew R. Blaustein, Armand M. Kuris, Jose Javier Alio

Source: *The American Naturalist*, Vol. 122, No. 4 (Oct., 1983), pp. 556-566

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/2461207>

Accessed: 25/04/2011 16:45

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PEST AND PARASITE SPECIES-RICHNESS PROBLEMS

Recently, two lines of evidence have been presented supporting the hypothesis that insect pests accumulate rapidly (within ecological time) on introduced plant species and that area, rather than time since introduction, accounts for faunal size. Strong (1974*a*, 1974*b*) compared the number of pests on introduced British trees with the number of pests on native trees. Regression analyses of the log number of pests on log geographic range for all British trees (native plus introduced) showed that the relationship was positive and highly significant. The regression residuals for both the introduced and native trees were not differentially distributed about the regression line. Further, the date of introduction was not significantly correlated with number of pests for the introduced trees. Thus, Strong (1974*a*, 1974*b*) concluded that in the time since these trees were introduced they had accumulated the number of pests predicted for native trees of similar geographic ranges.

A second pair of studies (Strong 1974*c*; Strong et al. 1977) compared the number of pests on agricultural crops (cacao and sugar cane) from different political entities. In these studies Strong and colleagues noted that pests rapidly accumulated when these crops were introduced outside their regions of origin and that the pests in these areas were typically native insects that had apparently become recently adapted to these crop plants. Strong et al. (1977, p. 173) summarized these studies stating, "Since there are no conflicting data, and since no analysis for any system shows great lengths of time to influence species richness, we suggest there is little justification for the 'time hypothesis' . . . for host-parasite communities."

Discussing factors that influence pest and parasite species richness we (Kuris et al. 1980) criticized the data base used in Strong et al. (1977). Rey et al. (1981) replied that our contribution did not challenge or test their principal hypothesis that time since introduction is not a factor in the accumulation of insect pests and that the present geographic range determines the number of pests after a short period of time (less than 300 yr). Here we examine their tests of the time hypothesis. We find that their analysis of the British tree data is faulty and that their data may support the time hypothesis when properly analyzed. We concur, however, that their evidence from introduced agricultural crops does counter the time hypothesis. Consideration of pest faunas for other introduced plant species suggests, however, that this influence of time on accumulation of pests is not a general phenomenon.

INSECTS ON BRITISH TREES

It is apparent from several recent comments (Rey et al. 1981; Lawton et al. 1981; Claridge and Wilson 1982*b*) that our paper (Kuris et al. 1980) was inter-

puted as too pessimistic about the use of published species lists and species-area relationships in general. We stand by our critical comments concerning specific studies (e.g., Strong et al. 1977; Dritschilo et al. 1975; see our discussion in Kuris and Blaustein 1977). However, certain species lists are quite comprehensive and when critically inspected for applicability of the data to the problem (e.g., Cornell and Washburn 1979; Lawton and Price 1979; Claridge and Wilson 1982a) are suitable for tests of ecological theory. We noted this point previously (Kuris et al. 1980, p. 579) and reiterate it here. In particular, the British entomofauna is quite suitable for analyses of species richness problems (e.g., see the recent comparisons of faunal lists with knockdown samples obtained using a pyrethrum mix [Southwood et al. 1982]).

The insect fauna of British trees is an alluring data base for biogeographic analysis because it is well known (Claridge and Wilson 1978) and detailed range maps of the flora are available (Perring and Walters 1962; Perring 1968). Since Southwood (1961) suggested the species-area relationship, Strong (1974a, 1974b) and Southwood (1977) have statistically confirmed the relationship with regression and correlation analyses. The numbers of recent insect species feeding on trees have also been positively correlated with the number of Quaternary pollen records for this flora (Southwood 1961, 1977; Strong 1974a, 1974b; Claridge and Wilson 1978). Birks (1980) criticized this approach because the number of pollen records is a poor indicator of past abundance. He found insect species richness to be correlated with radiocarbon age for estimates of postglaciation records of trees in Britain.

These procedural problems aside, we agree with Strong that the introduction of trees to Britain provides a natural experiment to test whether insects accumulate asymptotically in ecological time. The native trees may be used as a control group despite possibly important differences in phylogeny, chemistry, etc. First, we ask if a significant species-area relationship exists for the native trees alone. Similarly, do the introduced trees alone exhibit a significant species-area relationship? If both groups show significant species-area regressions and their variances are homogeneous, an analysis of covariance can be conducted. If either or both regressions are not significant, a nonparametric test should be employed to compare these two groups.

Before this analysis can be performed, some important problems with the data base must be resolved. Our recalculations from the maps of floral range suggest that Strong's studies (1974a, 1974b, 1979; Strong and Levin 1979) include the range of the trees in Ireland, while Southwood (1977) excludes Ireland. For a direct comparison with Strong's studies we also include Ireland although the pest list was developed for Britain alone (Southwood, in littera). Since Ireland adds no additional insects, inclusion of ranges in Ireland inflates the scale of the independent variable. Strong (1975) corrects the area for one tree species and adds pest data for two more species.

Beyond these procedural problems, we have observed that the history of the British tree flora, the partial resolution of the insect pest list to tree species, and differences in the inclusiveness of certain floral range maps require a more refined analysis of the species-area statistics. We divided the British trees into five main groups (table 1).

TABLE 1

HISTORY OF BRITISH TREES USED IN ANALYSES OF INSECT SPECIES AREA RELATIONSHIPS

1A. Native species whose range has not been greatly extended by further planting

	<i>No. of Insects</i>	<i>Geographic Range (km²)</i>
<i>Alnus glutinosa</i> (alder)	90	29.35×10^4
<i>Corylus avellana</i> (hazel)	73	29.01×10^4
<i>Fraxinus excelsior</i> (ash)	41	31.82×10^4
<i>Prunus spinosa</i> (sloe)	109	28.00×10^4
<i>Sorbus aucuparia</i> (rowan)	28	24.45×10^4
<i>Acer campestre</i> (common maple)	26	12.68×10^4
<i>Juniperus communis</i> (juniper)	20	5.06×10^4

1B. Native species whose range has been greatly extended by further planting (Perring and Walters [1962] record the total range for these species.)

	<i>No. of Insects</i>	<i>Geographic Range (km²)</i>
<i>Malus sylvestris</i> (apple) ^a	93	16.51×10^4
<i>Fagus sylvatica</i> (beech)	64	27.11×10^4
<i>Carpinus betulus</i> (hornbeam)	28	6.83×10^4
<i>Ilex aquifolium</i> (holly)	7	24.77×10^4

1C. Native species for which Perring and Walters (1962) recorded only the original range, not the total range that has been greatly extended by cultivation and naturalization

	<i>No. of Insects</i>	<i>Geographic Range (km²)</i>
<i>Pinus sylvestris</i> (pine) ^b	91	14.80×10^4
<i>Taxus baccata</i> (yew) ^c	1	12.12×10^4

2. Native genera^d

	<i>No. of Insects</i>	<i>Geographic Range (km²)*</i>
<i>Quercus</i> (2 spp.) (oaks)	284	26.01×10^4
<i>Salix</i> (18 spp.) (willows)	266	32.25×10^4
<i>Betula</i> (3 spp.) (birches)	229	26.05×10^4
<i>Crataegus</i> (2 spp.) (hawthorns)	149	31.99×10^4
<i>Populus</i> (3 spp.) (poplars)	97	19.69×10^4
<i>Ulmus</i> (6 spp.) (elms)	82	26.32×10^4

3. Species and genera once native to Britain that became extinct and were reintroduced

	<i>No. of Insects</i>	<i>Geographic Range (km²)</i>
<i>Picea abies</i> (Norway spruce) ^h	37	2.21×10^4
<i>Abies</i> spp. (firs) ^g	16	

4. Genus with both native and introduced species

	<i>No. of Insects</i>	<i>Geographic Range (km²)</i>
<i>Tilia</i> spp. (limes) ^e	31	13.98×10^4

TABLE 1 (Continued)

5. Introduced species		
	No. of Insects	Geographic Range (km ²)
<i>Larix decidua</i> (larch)	17	6.07 × 10 ⁴
<i>Acer pseudoplatanus</i> (sycamore)	15	31.50 × 10 ⁴
<i>Castanea sativa</i> (sweet chestnut)	5	9.85 × 10 ⁴
<i>Aesculus hypocastaneum</i> (horse chestnut)	4	16.94 × 10 ⁴
<i>Quercus ilex</i> (holm oak)	2	1.30 × 10 ⁴
<i>Juglans regia</i> (walnut) ^f h	3	1.10 × 10 ⁴
<i>Robinia pseudacacia</i> (acacia) ^f h	1	0.89 × 10 ⁴
<i>Platanus orientalis</i> (plane) ^f g	0	

NOTE.—Geographic ranges are from Perring and Walters (1962) and Perring (1968) and include Britain and Ireland. Number of pests are from Southwood (1961).

* Geographic ranges of the native genera used by Strong (1974a, 1974b) all substantially exceed our calculations from the same data source (Perring and Walters 1962) (see text).

^a *Malus* listed as a mixed genus of native and introduced species by Strong 1974b, p. 695 and treated statistically as native (p. 696).

^b *Pinus* excluded from analyses of Strong (1974a, 1974b).

^c *Taxus* included in analyses of Strong (1974a, 1974b).

^d Number of species in Perring and Walters (1962) given in parentheses.

^e Two native and one introduced species. The latter has a much more extensive geographic range than the native species.

^f Not analyzed by Strong (1974a, 1974b). Number of pests given in Claridge and Wilson (1978).

^g Geographic range not available.

^h Geographic range obtained from Southwood (1974).

Geographic range data should be comparably inclusive. (1) Range maps for some trees included extensive areas of domestic plantings beyond the native range (e.g., *Ilex aquifolium*) while maps for other species omitted localities outside the presumed native range even though Perring and Walters (1962) remarked that these additional plantings are extensive (e.g., *Taxus baccata*). With Strong (1974a, 1974b) we combined the native trees having extensive mapped domestic plantings with the native species whose range has not been so extended (1B with 1A of table 1). The time hypothesis would predict that species whose range has recently expanded would have fewer pests than predicted by a regression of insect species-richness on current geographic range because these tree species would not have had sufficient time to acquire the additional pests associated with increased geographic range. Distinction of native and introduced trees is more difficult when native trees with recently expanded ranges are included among the native trees. Therefore, the null of the time hypothesis is strengthened. Similarly, the lack of information on the current range of trees in 1C (table 1) mandated their exclusion from the analysis (Strong 1974a, 1974b excluded *Pinus* but included *Taxus*).

2. Previous analyses (Strong 1974a, 1974b, 1979; Strong and Levin 1979; Southwood 1977) did not distinguish between species and genera. Native trees included both single species (e.g., *Alnus glutinosa*) and genera with as many as 18

TABLE 2

LOG₁₀ SPECIES-LOG₁₀ AREA REGRESSION AND CORRELATION STATISTICS OF VARIOUS CATEGORIES OF BRITISH TREES (see table 1)

Groups of Trees	N	Slope	Intercept	F-Test	r
1A	7	.721	-2.154	5.651	.728
1A, 1B	11	.491	-.979	1.466	.374
1A, 1B, 1C	13	.765	-2.500	1.489	.345
1A, 1B, 2	17	.892	-2.925	4.570*	.483*
1A, 1B, 2†	17	.874	-2.898	11.050**	.653**
1A, 1B, 1C, 2	19	1.224	-4.753	5.104*	.481*
1A, 1B, 3	12	.264	.235	.895	.287
1A, 1B, 2, 3	18	.573	-1.209	3.779	.437
1A, 1B, 2, 3, 4	19	.589	-1.307	4.182	.444
5	7	.539	-1.871	6.636*	.755*
4, 5	8	.638	-2.262	7.862*	.753*
All	28	.988	-3.593	19.921**	.659**

* .01 < P .05.

** P < .01.

† Data for the genera are summed geographic ranges of the species from Strong (1974a).

species (*Salix*). The introduced trees are all single species (table 1). On a priori grounds the data for genera should be deleted from an analysis that otherwise compares native and introduced species. If there is any intrageneric host specificity by the insects, the number of insects recorded for the genera will be high compared to the hosts which are single species. This will introduce a bias toward higher correlations and greater slopes.

It should also be noted that the areas reported by Strong (1974a, 1974b, 1979; Strong and Levin 1979) for all British trees listed as genera are summations of the geographic ranges of all species in the genus (see also Claridge and Wilson 1982b). For *Salix*, the summed area is more than three times greater than the area of Great Britain. This procedure causes difficulties for interpretation, which we resolve by simply using the geographic range of the genus. The statistical effect of using summed geographic ranges reduces the slope and superficially seems to underestimate the importance of area. However, comparison of the effects of two sets of geographic ranges for genera (table 2) on the species-area relationship shows that the summed range data increases the significance of both the correlation coefficient and F-statistic. This was true for all tests involving generic data (only 1 comparison is shown in table 2). Because the scale of the independent variable, area, is greatly increased by using summed ranges, an outlier effect is created. Oddly, Strong and Levin (1979) use these summed generic ranges for the British trees but apparently do not do so for North American trees, despite their direct comparison of these two species-area relationships.

3. One species (*Picea abies*) became extinct in the postglacial period and was reintroduced in historic times according to Southwood (1961). Its status is therefore somewhat novel.

4. One genus (*Tilia*) includes two native species with restricted ranges and one widespread introduced species. Reasoning as for (2) above we exclude this genus on an a priori basis.

The influence of species richness data for these various groups of trees on the regression and correlation statistics has been analyzed by sequentially adding groups (2), (3), and (4) to the native tree species and group (4) to the introduced tree species (table 2). When native tree species alone are considered, no significant species-area relationship is apparent. When native tree genera are included with native tree species a significant relationship ($.025 < P < .05$) emerges. As predicted, the slope of the regression increases when genera are added because the genera have more insects per unit area. Adding data for the reintroduced tree (3) and mixed genus (4) makes the native tree relationship nonsignificant. However, the number of pests recorded from introduced trees is significantly associated with geographic range whether or not the mixed genus is included. In agreement with Strong (1974*a*, 1974*b*), including all trees yields a significant overall relationship. This appears to be caused by including the introduced species, most of which have small areas and few insects with the native genera which have large areas and many insects. Thus, counter to the claims of Rey et al. (1981, 1982), it is evident that data processing procedures can cause substantial statistical biases and may lead to very different conclusions (see also Kuris et al. 1980, p. 576).

The significant regression for introduced trees suggests that area is a potentially important determinant of insect species accumulation on these trees over the 300–1,900 years since these trees were introduced. Yet, for the native trees no such relationship is apparent and other causes for differences in species richness must be sought (A. Kuris, A. Blaustein, and J. Alió, in prep.).

Finally, we can ask if the introduced trees have acquired as many insects as have native trees. A comparison of the insect numbers for the native and introduced trees (fig. 1) shows that 10 of the 11 native trees lie above the regression line for the introduced trees. For a statistical comparison of these data we first combine both groups for a regression analysis (\log_{10} number of insect pests = $0.887 \log_{10}$ geographic range - 3.23), F -test = 20.95 ($.01 < P < .05$), $r = 0.75$ ($.01 < P < .05$) as did Strong (1974*a*). A Mann-Whitney U -test of the residuals shows that native trees have a significantly greater number of insects ($.01 < P < .025$) than do the introduced trees. Thus, these data show that time may be an important factor. Introduced trees require more than 300–1,900 years to acquire insect numbers comparable to native trees. We suggest that introduced trees may quickly acquire polyphagous generalists. Specialist herbivores either have to evolve the ability to feed on introduced plant species or must themselves be introduced. Thus, specialists should accumulate slowly. Local specialists (*sensu* Fox and Morrow 1981) are herein regarded as specialists if the mechanism for such specialization is physiologic, as generalists if the mechanism is ecologic.

A flora (including introduced species) exhibits varying degrees of coevolved relationships with its associated entomofauna. (1) Generalist insects may rapidly spread to suitable introduced plants without evolutionary modification. The pests

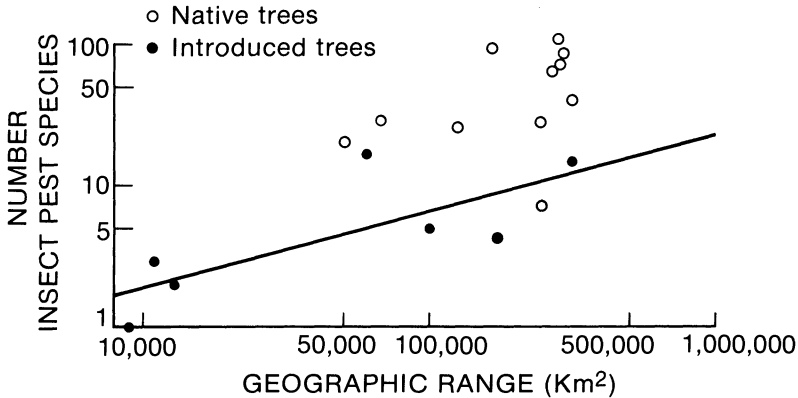


FIG. 1.—Relationship of \log_{10} number of insect pests and \log_{10} geographic range for native trees (1A and 1B of table 1) and introduced trees of the British Isles. The regression line (\log_{10} number of insect pests = $0.539 \log_{10}$ geographic range - 1.871, $F = 6.64$ [$.01 < P < .05$], $r = 0.76$ [$.01 < P < .05$]) includes only the introduced trees.

of nonnative sugar cane studied by Strong et al. (1977) may include many such species. (2) Specialist insects spread to and become important pests on new hosts following evolutionary changes in nutritional physiology or increased synchronization of their life cycle with that of their host. Evidence for such evolutionary changes is now well documented and includes the establishment of the tephritid fruit fly *Rhagoletis pomonella* on orchard crops (Bush 1975) and the development of populations of scale insects (*Nuculaspis californica*) that are specialized feeders on individual ponderosa pine trees (Edmunds and Alstad 1978). (3) As the number of pests accumulates on a host plant, ultimately either the pest fauna as a whole or a few particular (perhaps specialist) pest species will cause sufficient damage to select for a coevolutionary response by the plant. Thus, some of the pest species may no longer be able to feed on such plants, or insect density may be decreased.

An intensive study by Love (1980) comparing pest associations of a native and introduced species of hawthorn (*Crataegus*) further illustrates our points on specialist-generalist accumulation rates. In Oregon, Love (1980) censused insect pests on both a native (*C. douglasii*) and an introduced species (*C. monogyna*; introduced about 100 yr ago) to test the hypothesis that insect species accumulation on an introduced plant will reach equilibrium in ecological time (Strong 1974b; Strong et al. 1977).

Love's (1980) observations supported the hypothesis that the insect species richness of an introduced tree species would approach the level of native trees since the numbers of insects found on each species were similar. Her observations were also consistent with our coevolutionary hypothesis, however, because a closely related (congeneric) relative was available in the same habitat (see discussion in Connor et al. 1980). Thus, even most native hawthorn specialists were recorded on the introduced species (Love 1980).

Furthermore, Love (1980) found that densities of the most abundant herbivores (lepidopteran and sawfly larvae) were significantly higher on the native species. This was associated with significantly greater consumption of the native plant foliage during the spring, indicating that a number of common hawthorn pests fed preferentially on the native species.

Love (1980) also found that most of the insect species eating hawthorn foliage were generalists, feeding on a number of plant families or on a number of genera and species within the family Rosaceae. Some others were stenophagic, such as two gall-forming midge species (Diptera: Cecidomyiidae). These specialized midges were almost exclusively found on the native hawthorn and were responsible for substantial damage to the native species. These findings support the hypothesis that specialist pests are slower than generalists to colonize an introduced plant even though insect species richness may be equivalent for native and introduced species.

RAPID PEST SPECIES ACCUMULATION ON INTRODUCED PLANTS IS NOT A GENERAL PHENOMENON

Strong (1974c) and Strong et al. (1977) have stated that when cacao and sugar cane are introduced as cultivars to new regions, many pests are recruited from the insect fauna of the new area. Their analysis indicates that time since introduction is not a factor and that present geographic range soon determines the number of pests found on an introduced species. Abundant evidence from other plant introductions indicates however, that some introduced plants acquire very few new insect pests. In this relatively pest-free new environment such plants show an improved performance in terms of growth and survival.

Introduction of *Pinus radiata* (the Monterey pine) provides an example of our point. This tree is one of the most widely planted exotic forest crops in the world (Ohmart 1980). Extensive exotic *P. radiata* forests are now found in Chile, New Zealand, Spain, Italy, and Australia (Ohmart 1980). Dates of introduction are known for Australia and New Zealand which began planting *P. radiata* in the 1860s or 1870s (C. P. Ohmart, personal communication).

The Australia and New Zealand areas under cultivation are 480,000 ha and 740,000 ha, respectively (Ohmart 1980; Fenton 1979 for statistics). California has only about 8,000 ha of native *P. radiata* and about 3,000 ha of Christmas tree plantations (Ohmart 1980, personal communication). Ohmart (1981) found 319 species of insects on *P. radiata* growing in the native and domestic stands in California. Of these, he considers 88 as "casual visitors," which were probably only resting on the tree when collections took place; 146 species fed on the tree and 67 were predators or parasites of species associated with *P. radiata*. The relationship of the remaining species could not be determined. Although *P. radiata* has been present for over 100 yr in Australia and New Zealand, and plantations in these countries are orders of magnitude larger than the recent native distributional range in California, exotic plantings of *P. radiata*, in general, have been relatively pest free (Ohmart 1980). Occasional local outbreaks of indigenous insects have been recorded but Ohmart (personal communication) states that

insect grazing on exotic plantings of *P. radiata* is "very low." There are other documented examples supporting our points that newly introduced plants do not necessarily accumulate pests rapidly within ecological time and that pest pressure is much more intense on plants in their native areas (see e.g., Butterfield 1935; Morrow 1977; Morrow and Fox 1980; Zacharin 1978 for information on *Eucalyptus* trees; and Debach 1974; Dodd 1940; Moran 1980; Krebs 1978 for *Opuntia* cactuses).

CONCLUSIONS

By using the insect fauna of British trees as the data base for our biogeographic statistical analysis, we present evidence, in agreement with Strong (1974a, 1974b), that the geographical range of an introduced host plant can be an important determinant of the number of pests species it has acquired. We also show, however, that management of such data without a rationale that includes an examination of underlying assumptions can lead to statistical bias and substantially different conclusions. Our analysis suggests that native trees have significantly more insect pests than introduced trees. Therefore, time since introduction may also be an important factor influencing pest accumulation rates. We also suggest (with Gilbert 1979) that generalist pests are probably acquired more quickly than specialists and we present data that native host species can be under significantly more intense pest pressure than introduced species. Finally, while rapid accumulation of pest species on some host plants occurs, such a pattern of acquisition is not a general phenomenon.

ACKNOWLEDGMENTS

We thank A. Boucot, D. Breitburg, L. Fox, S. Gaines, D. Hews, M. Keough, D. Olson, C. Rinaldo, W. Schlesinger, E. Schoffelen, W. Sousa, and G. Wellington for their helpful comments on the manuscript. Discussions with R. Love, P. McEvoy, C. Ohmart, F. Rickson, and D. Smith greatly enhanced this paper and we thank T. R. E. Southwood and M. F. Claridge for enlightening us about some details of the data base for British insects and trees. We especially thank C. Ohmart for allowing us to use his unpublished data and D. Strong for frank and lively discussions on this and related matters. J. J. A. thanks the Fundación Gran Mariscal de Ayacucho for financial support. The comments of anonymous reviewers greatly improved the manuscript. Publication costs were defrayed by NSF grant BNS 8120203 to A. R. B.

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ANDREW R. BLAUSTEIN

DEPARTMENT OF ZOOLOGY
OREGON STATE UNIVERSITY
CORVALLIS, OREGON 97331

ARMAND M. KURIS
JOSÉ JAVIER ALÍO

MARINE SCIENCE INSTITUTE AND
DEPARTMENT OF BIOLOGICAL SCIENCES
UNIVERSITY OF CALIFORNIA
SANTA BARBARA, CALIFORNIA 93106

Submitted May 13, 1982; Revised November 29, 1982; Accepted April 6, 1983