

Role of plant abundance in determining the abundance of herbivorous insects

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Summary. The proposal (Gaston and Lawton 1988a, b) that small species of insects are more abundant because they have lower per capita resource requirements than large species does not hold for aphids (Dixon 1990a). There are good theoretical grounds, supported by empirical data, for the suggestion that host specific aphids that live on uncommon plants incur great losses in finding their host plants and as a consequence have a lower realized r_m and are rarer than aphids living on common plants. This is also likely to apply to other organisms that are host specific and 'time-limited' dispersers.

Key words: Abundance – Dispersal – Herbivorous insects – Plant cover

Gaston and Lawton (1988a, b) and Lawton (1989) have proposed that small species of insects are more abundant because they have lower per capita resource requirements than large species. Although this may hold when comparing generalist species of a range of sizes from different taxa, there is no evidence for it at the level of a taxum (c.f. Dixon 1990a). For example, both the field maple (*Acer campestre*) and sycamore (*Acer pseudoplatanus*) have similar sized host specific aphids that belong to the same genus (*Drepanosiphum aceris* and *D. platanoidis*), have similar intrinsic rates of increase (unpublished results) and are attacked by the same hymenopterous parasites (P. Stary, personal communication) and predators. However, *D. aceris* is much less common per unit area of leaf of field maple than is *D. platanoidis* on sycamore (Stroyan 1977). If the marked differences in abundance of these two species of aphid cannot be accounted for in terms of either the efficiency of their natural enemies or their intrinsic rate of increase, what determines the difference in abundance?

The equilibrium population density of a species is

seen as the outcome of the interaction between its rate of increase and the strength of the density dependent factors acting upon it. Natural enemies do not appear to have a great role in regulating the abundance of tree-dwelling aphids (Dixon 1985, 1990b). Moreover there is no evidence that the efficiency of the natural enemies of species differ (see above). Therefore, differences between aphid species in r_m , or more particularly realized r_m , appear to be the most likely cause of differences in abundance between species. Prey-predator and host-parasite models predict that an increase in the r_m of the host (or prey) will result in an increase in the equilibrium density of the host (or prey), provided all other factors remain constant (Hassell 1978). Thus, even if natural enemies have a role in determining aphid abundance, their population density would be positively correlated with r_m .

To illustrate the effect of an herbivore's r_m on its abundance, an appropriate plant herbivore model, which has some similarity with plant aphid interactions, is the laissez-faire model of Caughley and Lawton (1981):

$$\begin{aligned} dV/dt &= r_1 V(1 - V/K) - C_1 H[1 - \exp(-d_1 V)], \\ dH/dt &= H\{-a + C_2[1 - \exp(-d_2 V)]\}, \end{aligned} \quad (1)$$

where V = plant abundance, H = herbivore abundance, r_1 = intrinsic rate of increase of the plants, K = maximum possible plant density or biomass, C_1 = maximum rate of food intake per herbivore, d_1 = searching efficiency of the herbivore when food is scarce, a = rate of decline in abundance of herbivores in absence of food, C_2 = rate at which a is ameliorated by abundant food, d_2 = ability of the herbivore to multiply when food is scarce. This gives equilibrium densities for the plant (V^*) and herbivore (H^*) of:

$$\begin{aligned} V^* &= (1/d_2) \ln [C_2/C_2 - a], \\ H^* &= \frac{r_1 V^*(1 - V^*/K)}{C_1 [1 - \exp(-d_1 V^*)]}. \end{aligned} \quad (2)$$

C_2 in this model is roughly equivalent to r_m (if $a \ll C_2$). An increase in C_2 results in an increase in the equilibrium density of the herbivore providing V^* is close to

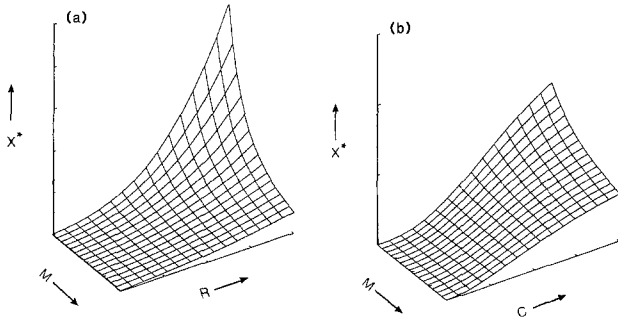


Fig. 1 a, b. A three dimensional surface (a) from Eq. (7) showing the dependence of the equilibrium density (X^*) on both the strength of the density dependent factor(s) (M) and the magnitude of the realised r_m (R), and (b) from Eq. (11) showing the dependence of the equilibrium density (X^*) on both the strength of the density dependent factor(s) (M) and plant cover (C)

$K/2$. This is particularly the case for tree dwelling aphids, which are unlikely to affect the equilibrium density of their host plants very much, if at all. Aphid population dynamics, however, are more complicated than Caughley and Lawton's model assumes, because the between year dynamics is discrete rather than continuous. The significance of this will be discussed in a future paper.

Thus there are good theoretical grounds for expecting a positive correlation between r_m and abundance. The analysis of empirical data for three species of tree dwelling aphids reveals that the relationship between peak spring (S) and autumn (A) abundance on a log-log scale is:

$$\text{Log } A = \text{log } S + \text{log } R - M \text{log } S \quad (3)$$

where R is the realized rate of increase and M the density dependent factor. The latter includes both the effect of natural enemies and intra-specific competition for food. Spring abundance can roughly be equated with abundance the previous autumn (Dixon 1985, 1990; Gange 1985)). This gives the following difference equation for the between year dynamics:

$$\text{Log } X_{t+1} = \text{log } X_t + \text{log } R - M \text{log } X_t \quad (4)$$

where X_t and X_{t+1} are the peak numbers in spring of years t and $t+1$, respectively, which after delogging gives:

$$X_{t+1} = R X_t^{1-M} \quad (5)$$

The equilibrium density (X^*) of which is:

$$X^* = R X^{*1-M} \quad (6)$$

or

$$X^* = R^{1/M} \quad (7)$$

Thus the empirical data for deciduous tree-dwelling aphids also indicate that differences in abundance could be determined by differences in realised r_m (R , Fig. 1 a).

Host plant abundance

What factors are likely to affect the degree to which r_m is realised? If there are no density dependent factors

operating on a population, then the between year dynamics can be represented by:

$$X_{t+1} = P(C) r X_t \quad (8)$$

Where $P(C)$ is the probability of finding a host plant assuming aphids disperse at least once a year ($P(C)$ is an increasing function of the relative cover of the host plant, C) and r is the maximum potential growth rate (Dixon et al. 1987). Thus, the realized intrinsic rate of increase, R , which includes the losses incurred in dispersal, is:

$$R = X_{t+1}/X_t = r P(C) \quad (9)$$

Thus R increases as plant cover (C) increases. For example, given that the probability of finding a host plant [$P(C)$] after D trials (Dixon et al. 1987) is:

$$P(C) = 1 - (1 - C)^D \quad (10)$$

then the equilibrium density is given by:

$$X^* = \{r[1 - (1 - C)^D]\}^{1/M} \quad (11)$$

This indicates that, all other things being equal, the proportional cover of the host plant through its effect on realised r_m can markedly affect the abundance of an aphid (Fig. 1 b).

Empirical data

Although the abundance of very few aphids has been determined, nevertheless, taxonomists have considerable experience of collecting aphids over wide areas and sometimes give qualitative estimates of aphid abundance. One such data set is that of Stroyan (1977) for the indigenous deciduous tree-dwelling aphids of Britain, which all belong to the same family, the *Callaphididae*. They are either highly host specific or live on at most two species of a particular genus of trees. When more than one species occurs on a tree, the commonest species has been selected, as the rarer species is usually confined to plants growing under particular conditions like deep shade. Population studies on six of the twelve species indicates that they are very similar in terms of their dynamics and the value of the density dependent component (Dixon 1970, 1971, 1990; Heie 1972; Sluss 1967; Gange 1985). The abundance of the trees is based on the impressions of Dr. O. Rackham. The relation between the ranked abundance of tree-dwelling aphids and that of their host plants is given in Fig. 2.

That abundant aphids tend to live on abundant trees lends support to the idea that plant abundance is a major factor determining aphid abundance.

Discussion

There are good theoretical grounds, supported by empirical data, for arguing that a major factor determining the abundance of tree-dwelling aphids is the abundance of their host trees. This is likely to apply to other organisms that are host specific and 'time-limited' dispersers

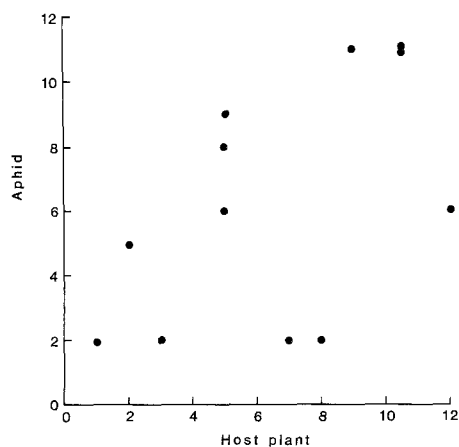


Fig. 2. The rank abundance of twelve species of Callaphididae in relation to the rank abundance of their host trees (Aphids: *Callaphis juglandis* (Goeze); *Drepanosiphum aceris* Koch; *D. platanoidis* (Schrank); *Eucallipterus tiliiae* (L.); *Euceraphis punctipennis* (Zett.); *Myzocallis boeneri* Stroyan; *M. carpini* (Koch); *M. castanicola* Baker; *M. schreiberi* H.R.L. & Stroyan; *Phyllaphis fagi* (L.); *Pterocallis alni* (DeGeer); *Tuberculooides annulatus* (Hart.); $r_s = 0.61$, $Z = 2.02$, $P < 0.05$)

(Ward 1987) like aphids. It follows from the idea put forward by Dixon et al. (1987) to account for the world wide distribution and species diversity of aphids. Not only does the proportion of ground covered by each species of plant have to exceed a certain critical level if it is to support an aphid species, but the greater the proportional cover the more abundant is its aphid. The high abundance of many pest species of aphids may similarly be seen as partly a consequence of the high proportional cover of their host plants (crops).

Our approach has greatly simplified the problem by ignoring confounding factors like habitat fragmentation (Rabinowitz 1981; Kareiva 1987). However, it does indicate that plant abundance could be important in determining the abundance of certain herbivores, a role previously not attributed to plants. If correct, it needs to be borne in mind when attempting to preserve the habitats of such organisms. It also serves to highlight the selective advantage of reduced dispersal when host plants are uncommon. A decrease in the abundance of a host plant could have been a major factor in the evolution of apterousness in aphids as it not only results in an increase in r_m (Dixon 1972), but would also greatly reduce the losses incurred in dispersal. That the tendency to produce brachypterous forms, the first step in the evolution of apterousness, is shown only by the rarest

of British Callaphidinae, *Drepanosiphum dixonii*, supports this idea.

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References

- Caughley G, Lawton JH (1981) Plant-Herbivore Systems. In: May RM (ed) *Theoretical Ecology* 2nd. Blackwells, Oxford
- Dixon AFG (1970) Stabilization of aphid populations by an aphid induced plant factor. *Nature* 227:1368–1369
- Dixon AFG (1971) The role of intra-specific mechanism and predation in regulating the numbers of the lime aphid *Eucallipterus tiliiae* 1. *Oecologia* 8:179–193
- Dixon AFG (1972) Fecundity of brachypterous and macropterous alatae in *Drepanosiphum dixonii* (Callaphididae, Aphididae). *Entomol Exp Appl* 15:335–340
- Dixon AFG (1985) *Aphid Ecology*, Blackie, Glasgow, p 157
- Dixon AFG (1990a) Ecological interactions of aphids and their host plants. In: *Aphid-Plant Genotype Interactions*. Campbell RK, Eikenbary RD (eds). Elsevier, Amsterdam New York
- Dixon AFG (1990b) Population dynamics and abundance of deciduous tree-dwelling aphids. In: *Population Dynamics of Forest Insects*. Hunter M, Kidd N, Leather S, Watt A (eds). Intercept
- Dixon AFG, Kindlmann P, Leps J, Holman J (1987) Why there are so few species of aphids, especially in the tropics. *Am Nat* 129:580–592
- Gange AC (1985) The ecology of the alder aphid (*Pterocallis alni* (Degeer)) and its role in integrated orchard pest management. PhD Thesis, University of London, p 556
- Gaston KJ, Lawton JH (1988a) Patterns in the distribution and abundance of insect populations. *Nature* 331:709–712
- Gaston KJ, Lawton JH (1988b) Patterns in body size, population dynamics, and regional distribution of bracken herbivores. *Am Nat* 132:662–680
- Hassell MP (1978) *The dynamics of arthropod predator-prey systems*. Princeton University Press, Princeton, p 237
- Heie OE (1972) *Bladlus pa birk i Danmark* (Hon., Aphididae). *Ent Medd* 40:81–105
- Kareiva P (1987) Habitat fragmentation and the stability of predator-prey interactions. *Nature* 326:388–390
- Lawton JH (1989) What is the relationship between population density and body size in animals? *Oikos* 55:429–434
- Rabinowitz D (1981) Seven forms of rarity. In: *The Biological Aspects of Rare Plant Conservation*. Syne H (ed). The biological aspects of rare plant conservation. John Wiley & Sons Ltd, pp 205–217
- Sluss RR (1967) Population dynamics of the walnut aphid *Chromaphis juglandicola* (Kalt.) in northern California *Ecology* 48:41–58
- Stroyan HLG (1977) Homoptera Aphidoidea (Part) Chaitophoridae and Callaphididae. *Roy Ent Soc Lond. Handbooks for the Identification of British Insects Vol. 11, Part 4(a)*, p 130
- Ward SA (1987) Optimal habitat selection in time-limited dispersers. *Am Nat* 129:568–579