

Testing models for equilibrium distribution and abundance of insects

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Abstract: The Kean–Barlow model predicts how the equilibrium distribution and abundance of a population may be affected by local rates of increase, dispersal, colonisation, and extinction. Here, the model is parameterised for three insects: the Glanville fritillary *Melitaea cinxia* in Åland, Finland, the ribbonwood aphid *Paradoxaphis plagianthi* in Christchurch, New Zealand, and the coxella weevil *Hadramphus spinipennis* in the Chatham Islands, New Zealand. The model was modified for the weevil to accommodate its unusual habit of overexploiting local resources. For the butterfly and the weevil, parameters estimated from the literature suggest high patch occupancy with low to moderate relative local population sizes. For the aphid, the model suggested low distribution and abundance. These predictions appear to match field observations, at least qualitatively, suggesting that the model captures sufficient biological detail to be a valid tool for exploring the relative effects of population-level processes on rarity and commonness.

Keywords: Rarity; dispersal; metapopulation dynamics; *Melitaea cinxia*; *Paradoxaphis plagianthi*; *Hadramphus spinipennis*.

Introduction

In the paradoxical words of Brian McArdle (1990, p. 276), “Rare species are very common”. This is true at both the community level, where the “mystery of singletons” is well recognised (Novotný and Basset, 2000), and on a landscape scale, where frequency histograms of species in terms of their global distribution or total numbers tend to be skewed towards the low end, with most species having low overall distribution or abundance (Gaston, 1994). Nevertheless, ecological theory has been built largely on observations of common species (Andrewartha and Birch, 1954), since these are generally easier to find and study, and are often of economic importance as pests.

Recently, however, rarity has become a subject for research in its own right (e.g. Rabinowitz, 1981; Gaston, 1994), with the predominant approach being to compare the biological characteristics of rare species with those of common relatives (e.g. Hodgson, 1993; Kunin and Gaston, 1997). This method leads to an interesting list of correlates to rarity, but it cannot on its own distinguish the mechanistic causes of rarity. Kean and Barlow (2004) suggested an alternative, based on a simple population model for local increase within habitat patches, coupled with local extinction and recolonisation between patches. The model predicts how each of seven general population parameters, including the local rates of increase, dispersal, and extinction, may affect the equilibrium distribution and relative abundance of a population within a mosaic of

habitat patches. Based on their equilibria, populations may be classified as: (1) common, if both distribution and local abundance are high; (2) localised, if distribution is narrow but local abundance is high where present; (3) sparse, if distribution is wide but local abundance is low; and (4) scarce, if both distribution and abundance are low. The latter three may be considered types of rarity (Rabinowitz, 1981).

The strengths of the Kean–Barlow model lie in its simplicity and objectivity. Each of the seven model parameters is biologically meaningful and measurable, and the assessment of whether a species is rare or not is made relative to the capacity of its environment rather than to an arbitrary set of other species. The weaknesses of the Kean–Barlow approach are that not all parameters may be easy to measure, conclusions may be too general to usefully inform management of a particular species, and the model has yet to be validated against a range of real populations. This contribution addresses the latter, using three well-studied insect species.

Methods

Kean–Barlow model for distribution and abundance

Kean and Barlow (2004) take a metapopulation approach, considering the distribution and relative abundance of a species by assuming it is distributed as a series of local populations across a large number of

habitat patches. The distribution may then be quantified as the proportion of available habitat patches that are occupied, P , while abundance is measured as the mean local population size where present, N , relative to the patch carrying capacity, K . Both P and N/K are values between 0 and 1, and provide a simple way of quantifying rarity: species with high N/K and P being designated common; those with high N/K but low P being localised; species with low N/K and high P being sparse; and those with low N/K and low P designated scarce (Kean and Barlow, 2004).

The model assumes that local populations increase independently and asynchronously from each other, but are linked loosely through dispersal. Occupied patches become empty through exogenous extinction events, with empty patches being colonised by randomly searching dispersers from occupied patches. The model is

$$\begin{aligned} \frac{dN}{dt} &= rN \left(1 - \frac{N}{K} (1 + v^2) \right) - mN(1 - \alpha P) \\ \frac{dP}{dt} &= c\alpha mNP(1 - P) - \varepsilon P \end{aligned} \quad (1)$$

where r is the intrinsic rate of local population increase, v^2 is the squared coefficient of variation between local population sizes, m is the dispersal rate, α is the survival rate of dispersers, c measures colonisation ability as the rate of successful establishment per immigration event, and ε is the density-independent local extinction rate. It should be emphasised that the model is not intended for simulation of a particular system, but rather as a mean field approximation for the average interactions within and between a series of local populations. Hence, the variation in local population sizes, an emergent property of real metapopulations, is here regarded as a constant model parameter v^2 arising from the averaging process together with Taylor's power law, as described by Kean and Barlow (2004). Similarly, several of the other model parameters represent the aggregated effects of lower-level population processes such as births, deaths, and dispersal.

The model may be solved for its equilibrium solutions N^*/K and P^* , which arise at the intersection between the isoclines:

$$\begin{aligned} P^* &= \frac{N^* \left((1 + v^2) - (1 - f) \right)}{\alpha f} \\ P^* &= 1 - g \left(\frac{N^*}{K} \right)^{-1} \end{aligned} \quad (2)$$

where $f = m/r$ is the emigration rate relative to the maximum rate of local increase, and $g = \varepsilon/c\alpha mK$ represents potential patch turnover as the extinction

rate of an occupied patch relative to the maximum colonisation rate of an empty patch. Exploring the effects of the parameters on the equilibrium abundance and patch occupancy led Kean and Barlow (2004) to infer some of the ecological circumstances that predispose species to rarity or commonness. The robustness of these conclusions depends on how well the model captures relevant population-level processes. By parameterising, and where necessary modifying, the model for some well-studied insects, its predictions can be validated against field results to help assess the usefulness of the model as a tool for understanding rarity and commonness.

Species modelled

Glanville fritillary

The Glanville fritillary butterfly, *Melitaea cinxia*, has been extensively studied across the Åland Archipelago in western Finland. Hanski *et al.* (1994) presented detailed data for a 50-patch metapopulation of *M. cinxia* studied in 1991–92. Mean estimated adult population size in 1991 across the 42 occupied patches was $N = 239$, with a squared coefficient of variation $v^2 = 2.18$. Of these, five had no larvae present the following spring, but only three had no adult butterflies when resurveyed subsequently in late summer, possibly because of adult dispersal immediately prior to the survey. The extinction rate of occupied patches can therefore be estimated at $3/42$ to $5/42$, or approximately 0.1 yr^{-1} .

Mark-recapture results from the same study suggested that the proportion of adults emigrating from a patch over a 9- to 16-day period (the longest span over which reliable estimates were possible) was 0.47 for males and 0.74 for females, suggesting $m = 0.6 \text{ yr}^{-1}$ on average. A similar mark-recapture study of the same species in a different patch network estimated an emigration rate of 0.4 (Kuussaari *et al.*, 1996), but this is likely to be an underestimate since a large proportion of the marked individuals (53% of males and 64% of females) disappeared, most likely through migration and subsequent mortality. This rate of disappearance does, however, allow us to estimate dispersal survival $\alpha \approx 1 - 0.6 = 0.4$. In the 50-patch metapopulation, five of the eight empty patches were colonised between 1991 and 1992 (Hanski *et al.*, 1994), so that the net rate of colonisation per empty patch was 0.625. The number of immigration events per empty patch may be estimated as $\alpha mNP/(1 - P)$, suggesting the probability of successful colonisation $c = 0.625/\alpha mNP = 0.013$. This estimate is considerably lower than the value of 0.5 used by Hanski and Thomas (1994), who assumed that half of the immigrants into an empty patch are mated females, but did not take into account the probability that these females successfully establish a viable local population. For reproductive rate, Hanski and Thomas

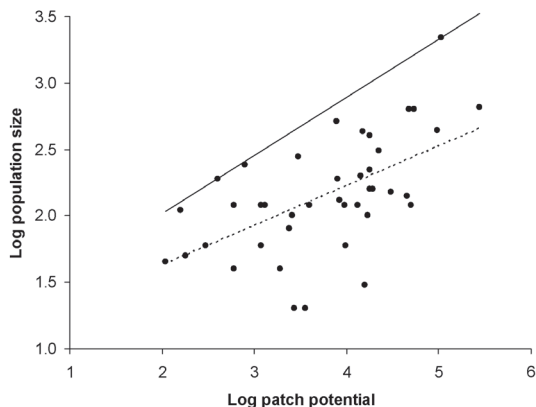


Figure 1. Relationship between local population size and patch potential (patch area multiplied by quality) for *M. cinxia* in a 50-patch metapopulation (data from Hanski *et al.*, 1994). Dotted line shows regression model fit ($y = 0.300x + 1.025$, d.f. = 41, $R^2 = 0.32$, $P < 0.001$); solid line is fitted through the observed maxima ($y = 0.437x + 1.143$).

(1994) assumed $r = 2.0 \text{ yr}^{-1}$, based on that measured for the closely related marsh fritillary, *Mellicta athalia* (Warren, 1991).

Estimating K for this system is difficult since habitat patches vary in both size and quality, and extinction/recolonisation dynamics mean that observed local population sizes do not necessarily reflect their local potential. The 1991 data for the 50-patch metapopulation (Hanski *et al.*, 1994) show a highly significant relationship between local butterfly population size and “patch potential”, given by patch area multiplied by an index of quality (Fig. 1). A line was fitted to the observed maxima, since this gives the best estimate of patch carrying capacities. This result suggests that populations in large, good-quality patches are no more likely to be close to K than those in small, poor patches, which is consistent with the model’s assumption that local extinctions are independent of population size or quality. The fitted function was applied to each of the 50 patches, and the results averaged to estimate the mean local carrying capacity as $K = 724$ for this metapopulation.

Ribbonwood aphid

The indigenous New Zealand ribbonwood aphid (*Paradoxaphis plagianthi* Eastop) lives year-round on the leaves and flower buds of the lowland ribbonwood tree, *Plagianthus regius*. Although its host is common throughout New Zealand, the aphid is known only from small stands of remnant lowland forest in the centre of Christchurch city (Kean, 2002). Within this

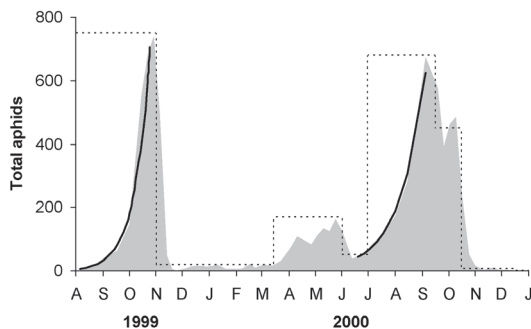


Figure 2. Temporal dynamics of a *P. plagianthi* subpopulation (shaded area), with exponential spring increase (solid lines: in 1999, $\log N = 0.90 + 0.024t$, $R^2 = 0.97$; in 2000, $\log N = 1.63 + 0.015t$, $R^2 = 0.99$, where t is time in days), and estimated carrying capacity fitted by inspection (dotted lines).

habitat, only a few small colonies have been observed at any one time, with the aphid absent from many apparently suitable hosts. Furthermore, when present, local populations occupy only a small proportion of the available and apparently suitable leaves (Kean and Stufkens, 2005), with no apparent differences in distribution from ground level to canopy (Marlon Stufkens, Crop & Food Research, Lincoln, N.Z., *pers. comm.*).

Field populations of the ribbonwood aphid have been monitored in some detail, allowing the model parameters to be estimated. The observed exponential rate of colony growth in spring (Fig. 2) was 0.024 in 1999 and 0.015 in 2000 (Kean and Stufkens, 2005), suggesting $r = 0.02 \text{ day}^{-1}$ on average. Field densities varied considerably, but consistently, throughout the year (Kean, 2002; Kean and Stufkens, 2005), probably reflecting seasonal changes in host plant quality, which can be regarded as setting the carrying capacity, K . A weighted seasonal mean was estimated as shown in Figure 2, suggesting $K = 261$ for this colony. At any one time, the largest number of local aphid colonies known was 11, on 22 February 2000, with sizes 1, 1, 1, 2, 3, 8, 11, 16, 23, and 53, suggesting $v^2 = 1.9$.

Dispersal rate, m , was estimated by noting that, on average throughout the year, 29% of fourth instar nymphs in field populations were winged (Kean, 2002). Since the rate of production of adults is r , the rate of production of alatae (winged adults) may be estimated as $m = 0.29r = 0.0057 \text{ day}^{-1}$. This assumes that all alatae disperse, but is reasonable given that very few were observed in the aphid colonies. To estimate

dispersal survival, α , it was first necessary to calculate approximately how many alates were produced in a field colony over the course of a year. While it was not possible to count them directly, since they tend to fly away, it was possible to infer them from knowledge of winged fourth instar numbers and their development time. Total nymphal development is split fairly evenly into four instars, and requires 212 degree days above a lower threshold of 5°C (Kean and Stufkens, 2005). Temperature in the field during the time of peak alate production in spring 2000 rarely dropped below the 5°C threshold, and the 11.6°C mean suggests a fourth instar development time of around 8 days. The area under the curve of winged fourth instar density over time was 707.5 for 2000, suggesting that $707.5/8 = 88$ alates were produced. During this season, 10 new colonies were observed in the vicinity of the main colony (Kean, 2002), therefore dispersal survival may be estimated as $\alpha = 10/88 = 0.11$. Of these 10 new colonies, only two survived to produce dispersers of their own, with the remainder going extinct at only one or two aphids (Kean, 2002). The probability of successful colonisation may be estimated directly, therefore, as $c = 2/10 = 0.2$. Conversely, the extinction rate may be estimated as the inverse of mean persistence time for the three colonies for which this is known (Kean, 2002): $\epsilon = 3/(489+92+40) = 0.005$ /day.

Coxella weevil

The coxella weevil (*Hadramphus spinipennis* Broun) is confined to two small islands in the Chatham group, New Zealand, where its host plant, Dieffenbach's spargrass *Aciphylla dieffenbachii*, is patchily distributed (Schöps, 2000). Weevil and host are classified as endangered and threatened, respectively, but management is complicated by the fact that weevil populations tend to overexploit their local resources causing the death of host plants and collapse of their habitat patch; weevils subsequently disperse up to 500 m to new patches (Schöps, 2002). Since both patch extinction rate and dispersal rate are dependent on local density, the model of Equation 1 must be modified. By assuming that the risk of extinction increases as the local population approaches its carrying capacity, then the extinction parameter ϵ may be replaced by $\epsilon' \times N/K$. An implicit assumption is that for each habitat patch destroyed, another one becomes available through recruitment of seedlings. The dispersal rate is scaled in the same way as extinction, by replacing m with $m' \times N/K$, and the model becomes

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} (1 + v^2) \right) - m' \frac{N^2}{K} (1 - \alpha P) \tag{3}$$

$$\frac{dP}{dt} = c\alpha m' \frac{N^2}{K} P(1 - P) - \epsilon' \frac{N}{K} P$$

The equilibrium model isoclines are now given by

$$P^* = \frac{(1 + v^2) + f' - \left(\frac{N^*}{K}\right)^{-1}}{\alpha f'} \tag{4}$$

$$P^* = 1 - g' \left(\frac{N^*}{K}\right)^{-1}$$

where $f' = m'/r$, and $g' = \epsilon'/c\alpha m'K$ and the equilibrium itself is

$$\frac{N^*}{K} = \frac{(1 - \alpha f' g')}{f(1 - \alpha) + (1 + v^2)} \tag{5}$$

It can be shown that this equilibrium is stable and ecologically realistic only if $\alpha f' g' \leq 1$, $\alpha(1 - g') - v^2/f \leq 1$, and $g'(1 + v^2 + f) \leq 1$.

For the coxella weevil, mark-recapture experiments conducted across three summers (Schöps, 2002) suggested an average annual finite rate of increase of 1.97 in rapidly increasing local populations. The intrinsic rate of increase may be estimated as the natural log of the mean finite rate of increase: $r = \ln(1.97) = 0.68 \text{ yr}^{-1}$. In the same study it was noted that once weevil densities exceed 18 per plant then overexploitation occurs and the resource inevitably collapses (Schöps, 2002). This suggests that the probability of extinction becomes unity when the carrying capacity is exceeded, and $\epsilon' = 1$. Nevertheless, weevils did not disperse immediately on reaching this density, but remained and continued to increase until only a small piece of stem remained on each plant, with up to 55 weevils clustered on it (Schöps, 2000). This suggests that the density-dependent dispersal parameter

Table 1. Parameter values estimated for the case study species, and model equilibrium results.

	<i>M. cinxia</i>	<i>P. plagianthi</i>	<i>H. spinipennis</i>
Parameter estimates			
<i>R</i>	2.0 yr ⁻¹	0.02 day ⁻¹	0.68 yr ⁻¹
<i>K</i>	724	261	448
<i>v</i> ²	2.18	1.9	1.66
<i>m</i> or <i>m'</i>	0.6 yr ⁻¹	0.0057 day ⁻¹	0.33 yr ⁻¹
α	0.4	0.11	0.68
<i>C</i>	0.013	0.2	0.5
ϵ or ϵ'	0.1 yr ⁻¹	0.005 day ⁻¹	1 yr ⁻¹
Model equilibrium results			
<i>N</i> [*] / <i>K</i>	0.25	0.25	0.35
<i>P</i> [*]	0.82	0.39	0.94
type of rarity	sparse	scarce	sparse to common

may be estimated as $m' = 18/55 = 0.33$.

Despite being flightless, dispersing weevils were observed to travel up to 500 m to new habitat patches, and 68% of weevils released 100 m from the nearest host plants were later recovered from hosts (Schöps, 2000), suggesting dispersal survival is at least $\alpha = 0.68$. Colonisation ability appears to be high, but in the absence of data we follow Hanski and Thomas (1994) who assumed that half of the immigrants into an empty patch are mated females, hence $c = 0.5$.

Johst and Schöps (2003) estimated the carrying capacity of each of the habitat patches present on Mangere Island, suggesting a mean of $K = 448$. Since no information is available on the variability in weevil subpopulation sizes, it is assumed to be similar to that

for the patch carrying capacities reported by Johst and Schöps (2003), suggesting $v^2 = 1.66$. Given the subjectivity and uncertainty around several of the parameter estimates for this and the other case study species, sensitivity analyses were carried out to determine how much influence these have on the model outcomes. The parameter values derived for each of the three case studies are listed in Table 1.

Results

The results from estimating the model parameters for each of the case study insects are shown in Table 1 and Figure 3. The model equilibrium for *M. cinxia* suggests

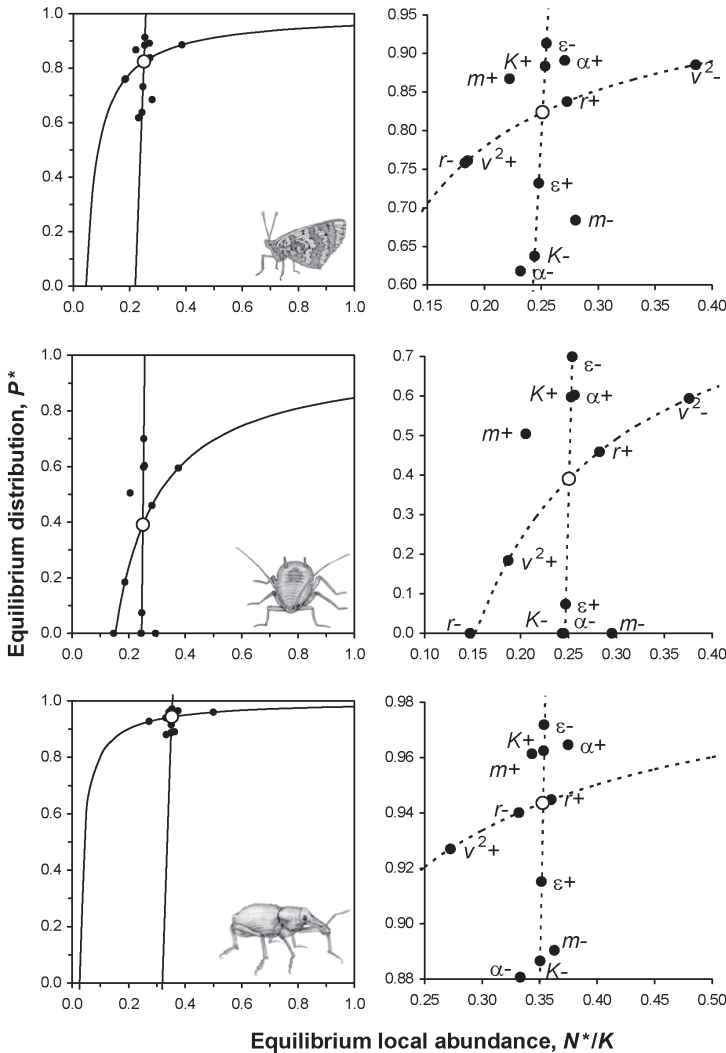


Figure 3. Results from parameterising the models for *M. cinxia* (top), *P. plagianthi* (middle) and *H. spinipennis* (bottom). Plots on the left show equilibrium isoclines (lines), with the stable equilibrium marked as an open dot; solid dots show the range of equilibria resulting from varying each equilibrium individually by 50%. Plots on the right are enlargements, labelling each of the sensitivity analysis results by the parameter altered by +50% (plus signs) or -50% (minus signs); results for parameter c are the same as for K .

high patch occupancy but low relative local abundance, and this was in close agreement with the actual values of $N^*/K = 239/724 = 0.33$ and $P^* = 42/50 = 0.84$ observed in the field in 1991 (Hanski *et al.*, 1994). The result was reasonably robust to substantial ($\pm 50\%$) variation in the model parameters, with the greatest effect arising from decreases in dispersal survival α , local carrying capacity K , colonisation ability c , dispersal rate m , or heterogeneity, v^2 (Fig. 3).

For *P. plagianthi*, the model suggested low equilibrium occupancy and relative abundance, and the result was sensitive to variation in the parameter values. The model suggested that 50% reductions in the intrinsic rate of increase r , local carrying capacity K , colonisation ability c , dispersal survival α , of dispersal rate m would eventually lead to extinction, while an equivalent decrease in local extinction rate ϵ would lead to a more widespread equilibrium population.

In contrast, the model for *H. spinipennis* suggested a wide distribution across habitat patches and moderate local abundance, with this result being very robust. Equilibrium occupancy and relative abundance was insensitive to the local rate of increase r , and affected little by $\pm 50\%$ changes in any of the other parameters. The greatest effect arose from reducing heterogeneity v^2 , leading to increased relative abundance.

Discussion

Kean and Barlow (2004) used their model to suggest what combination of population-level characteristics might predispose a species to a certain pattern of distribution and abundance. For *M. cinxia*, the model predictions of $N^*/K = 0.25$ and $P^* = 0.82$ appear to conform well with the actual values $N^*/K = 0.33$ and $P^* = 0.84$ observed in the field, despite there being some evidence that the metapopulation may not be at equilibrium (Hanski *et al.*, 1995). This comparison may be criticised on the grounds that the test was not completely independent since the estimation of model parameter c relied on the patch occupancy and local abundance observed in the field. However, the other six model parameters were estimated independently (though some indirectly from the same survey results) and sensitivity analysis suggested that the qualitative pattern of wide distribution and low relative local abundance was unaffected by substantial variation in the parameter estimates.

The same "sparse" pattern (Kean and Barlow, 2004) arises from the *H. spinipennis* model, though in this case the population equilibrium might even be classified as "common". Superficially, this might seem counter-intuitive for a species considered endangered by the New Zealand Department of Conservation

(Schöps, 2000), but the threat to the species is mainly perceived to be its very restricted natural range, being only two small rodent-free islands. Within those islands, however, the weevil is abundant (Schöps, 2000). This issue highlights the problems of unambiguously defining terms such as "rare" and "common", which have plagued ecology and hampered the development of robust theory. Rabinowitz (1981) made a major contribution by breaking "rarity" into a number of more specific types, and Kean and Barlow (2004) carried this further by suggesting how rarity might be quantified. The crux of the problem is that "rare" is a relative term: species may be rare in comparison with other species (Gaston, 1994), or compared with the capacity of their environment. The latter approach, embodied in the Kean–Barlow model, relies on the capacity of the environment being measurable, by defining suitable habitat patches and estimating the carrying capacity K of each. The current exercise has shown how difficult that can be, even for relatively well-studied species. As well as K , the occupancy and abundance predicted by the model for each of the case study species was sensitive to v^2 , which will be heavily influenced by the variation in size and quality of habitat patches. These difficulties help re-emphasise that the Kean–Barlow model is inappropriate for predicting specific solutions, with its value being rather as a tool for exploring the relative importance of population phenomena leading to particular patterns of occupancy and abundance.

The particular example of *H. spinipennis* also brings up the issue of populations affecting the availability or quality of their resources. The impacts of populations on their resources are well recognised in multi-trophic level studies, and exploited by biological control practitioners. *H. spinipennis* is perhaps unusual in the degree to which the resource is affected, with whole patches of host plants being destroyed, but the affect of a population on its resource makes it even more challenging to estimate the carrying capacity except by direct experimentation. Further developments on the population dynamics of rarity would benefit from consideration of population–resource interactions in more detail than the models discussed here.

Though no quantitative data are available for comparison, the model prediction of low equilibrium occupancy and abundance for *P. plagianthi* is consistent with its scarcity in the field, despite a high density of apparently suitable host trees (Kean, 2002; Kean and Stufkens, 2005). Comparison with the other case studies (Table 1) suggests that one of the main reasons for the rarity of *P. plagianthi* may be its very poor dispersal success, with only $\alpha = 11\%$ of dispersing aphids surviving despite host trees being particularly abundant in the forest where they are found. Dixon and

Kindlmann (1990) suggested that aphid densities might be determined partly by the abundance of their host plants in the landscape, mediated through dispersal mortality. If so, this might help to explain why *P. plagianthi* has not been found in other lowland forests, where a lower abundance of host trees might lead to even lower survival of dispersers in this weakly-flying species.

The sensitivity analysis suggested that *P. plagianthi* might be strongly affected by changes in its environment, with 50% reductions in any of local rate of increase r , dispersal rate m , carrying capacity K , survival on dispersal a , or colonisation ability c leading to overall extinction (Fig. 3). This should be of particular concern given the very restricted known range of this species. Conversely, the model suggests that a decrease in local extinction rate e or increases in K , c , or α might substantially increase patch occupancy. During 2000, an irrigation system was installed in Riccarton Bush, where this species is primarily found, and the model suggests that if this improves host tree quality or decreases local extinctions in the unfavourable summer months (Fig. 2) then there might be substantial benefits for the conservation of *P. plagianthi*. Conversely, the aphid may be vulnerable to habitat loss, as this would negatively affect several of the model parameters to which the species' persistence is sensitive (Fig. 3). This contrasts with the other case study species, which may be better able to withstand some habitat loss, and emphasises the need for better understanding of the determinants of rarity in order to gauge the likely impacts of human-induced change on different species.

In conclusion, the Kean–Barlow model suggests some insights into the population-level processes leading to the patterns of distribution and abundance seen in the three case study species. Parameterisation of the models was difficult in the absence of specially designed experiments, though sensitivity analyses suggested that the qualitative patterns suggested by the models were reasonably robust, at least for *M. cinxia* and *H. spinipennis*. The model predictions gave a qualitative match with field observations for each species, suggesting that the underlying assumptions may be appropriate, though further tests are recommended. Finally, it should be emphasised that the Kean–Barlow model and its variants are formulated as general tools for exploring distribution and abundance as ecological phenomena, but are not appropriate for making management decisions for particular species. Despite some suggestive results, these models are no substitute for detailed ecological study of rare species together with careful population viability analyses. With further empirical examples it may become possible to conduct comparative analyses that relate the critical model parameters to particular trait complexes of species. Meanwhile the management

of particular rare species should be informed by targeted study and strategic modelling, as is exemplified by the work on *M. cinxia* by Hanski and colleagues (e.g. Hanski and Thomas, 1994; Hanski, 1999) or on *H. spinipennis* by Johst and Schöps (2003).

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