

RESEARCH  
PAPER



# The portability of foodweb dynamics: reassembling an Australian eucalypt–psyllid–bird association within California

Julie L. Lockwood\* and James J. Gilroy†

\*Department of Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, NJ 08901, USA. †School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

## ABSTRACT

**Aims** To evaluate the role of native predators (birds) within an Australian foodweb (lerp psyllids and eucalyptus trees) reassembled in California.

**Location** Eucalyptus groves within Santa Cruz, California.

**Methods** We compared bird diversity and abundance between a eucalyptus grove infested with lerp psyllids and a grove that was uninfested, using point counts. We documented shifts in the foraging behaviour of birds between the groves using structured behavioural observations. Additionally, we judged the effect of bird foraging on lerp psyllid abundance using enclosure experiments.

**Results** We found a greater richness and abundance of Californian birds within a psyllid infested eucalyptus grove compared to a matched non-infested grove, and that Californian birds modify their foraging behaviour within the infested grove in order to concentrate on ingesting psyllids. This suggests that Californian birds could provide indirect top-down benefits to eucalyptus trees similar to those observed in Australia. However, using bird enclosure experiments, we found no evidence of top-down control of lerp psyllids by Californian birds.

**Main conclusions** We suggest that physiological and foraging differences between Californian and Australian psyllid-eating birds account for the failure to observe top-down control of psyllid populations in California. The increasing rate of non-indigenous species invasions has produced local biotas that are almost entirely composed of non-indigenous species. This example illustrates the complex nature of cosmopolitan native-exotic food webs, and the ecological insights obtainable through their study.

## Keywords

Australia, biological control, biological invaders, birds, California, eucalyptus, food webs, lerp psyllids, top-down effects.

\*Correspondence: Julie Lockwood, Department of Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, NJ 08901, USA. E-mail: lockwood@aesop.rutgers.edu

## INTRODUCTION

One of the principal by-products of a globalized economy is the transport, release and establishment of species outside of their native range (Cox, 1999; Van Driesche & Van Driesche, 2000). The rate at which particular locations are being invaded is accelerating (Mack *et al.*, 2000) such that some biotas are composed almost entirely of non-indigenous species (e.g. lowland Hawaii, central valley of California). Many of these co-occurring non-indigenous species originate from disparate regions and thus share no coevolutionary history, despite the fact that they interact in meaningful ways (e.g. a Brazilian scale insect tended by an African ant in Hawaii; Bach, 1991). However, by virtue of shared

transportation vectors or commonly travelled introduction pathways, species that co-occur within their native range may also co-occur within their introduced range, thereby re-assembling part of their native food web within a novel (non-indigenous) biological context. The integrity of 'native' associations within a non-indigenous context has received limited attention (Simberloff & Von Holle, 1999; Lohrer & Whitlatch, 2002). The few discussions that have taken place have viewed the issue solely through the lens of biological control (e.g. Hanks *et al.*, 2001). In particular, most invasion ecologists have overlooked the effect of these reassembled food webs on associated native species, especially in terms of possible indirect trophic effects (Simberloff & Von Holle, 1999). Here we compare a eucalypt–psyllid–bird association

between Australia, where it is native, and California, where it is non-indigenous. In particular, we compare the role that insectivorous birds play in mediating the negative effects of the psyllid on eucalypt trees between the two locations.

The majority of lerp psyllids (*Glycaspis* spp.; Homoptera; Psylloidea; Spondyliaspidae) are tightly associated with eucalypt forests within Australia (Moore, 1970; Majer *et al.*, 1997). Lerp psyllids play a significant role as primary consumers of eucalypt foliage, which is a particularly ligneous and unpalatable resource that is ignored by most potential herbivores (Majer *et al.*, 1997). Lerp psyllids themselves serve as a critical food resource for a variety of predators. Although eaten by a diverse range of insect predators (Dreistadt & Garrison, 1999), the relationship between lerp psyllids and bird communities is thought to be of greatest importance (Loyn *et al.*, 1983; Stone, 1996; Clarke & Schedvin, 1999). Most bird predation occurs when the psyllid is in its nymph stage. *Glycaspis* nymphs use their straw-like mouthparts to suck juices from the phloem vessels of leaves. All or part of the phloem is then deposited on the leaf surface as a protective cap known as a 'lerp', giving the group its distinctive name. These lerp (and associated nymphs) can occur at extremely high densities covering both surfaces of infested leaves. This resource provides birds with ample amounts of carbohydrates and other vital compounds (e.g. amino acids). If the lerp covering is eaten, and not the nymph, the nymph is capable of creating a replacement lerp covering in as little as one or two days (Loyn *et al.*, 1983). Thus in terms of the bird's food supply, lerp are a readily available, energetically rewarding, and constantly renewed resource.

In Australian eucalypt forests, lerp psyllid infestations are often closely associated with the presence of bell miner colonies (*Manorina melanophrys*). Colonies of this cooperatively breeding honeyeater (Meliphagidae) aggressively defend large territories (that include several eucalypt trees) against other birds, and thereby dramatically reduce the richness and abundance of other birds in the vicinity of their colonies. As a consequence, the presence of bell miners decreases predation on lerp psyllids by limiting the number and types of lerp predators. This in turn allows the lerp psyllid populations to reach comparatively high densities, thereby providing the bell miners with large supplies of their principal food source — the psyllid nymphs and their lerp coverings. Studies by Loyn *et al.* (1983) and Clarke & Schedvin (1999) show that the removal of bell miners increases predation on lerp psyllid populations by facilitating the entry of a diverse assemblage of nomadic birds. The positive effect of bell miner colonies on lerp psyllid populations is so large that the removal of bell miners, and the consequent influx of other birds, can reduce psyllid populations to non-infestation levels in as little as three months (Loyn *et al.*, 1983).

This mutualistic indirect relationship between birds, lerp psyllids and eucalypt trees has recently been reassembled within coastal California. Eight eucalypt species have become incorporated into California's flora, including the river red gum (*Eucalyptus camaldulensis*; Bossard *et al.*, 2000). Eucalypt trees were originally imported into California in the mid 1800 s. Early Californian foresters found that eucalypts grew easily and rapidly, and based on these experiences, several governmental agencies

promoted sowing eucalypt seedlings around farms and home-steads to serve as windbreaks, and in groves to provide ready sources of building material and fuel. Although eucalypts never lived up to their promise as economically valuable hardwood, many commercial growers persist in California and sell eucalyptus trees as ornamentals. This industry, combined with the natural expansion of many of the originally planted groves, has allowed several species of *Eucalyptus*, including the river red gum, to realize a broad distribution in California (Bossard *et al.*, 2000).

The red gum lerp psyllid (*Glycaspis brimblecombei*), a specialist phytophage on the river red gum (Moore, 1970), was first detected in Los Angeles in 1998. By 1999 it had been found over 500 miles north in the San Francisco Bay area (Dahlsten, 1999). As is the case in their native Australia, heavy infestations of the red gum lerp psyllid in California have resulted in increased rates of leaf abscission and a reduction in survival of affected eucalypt trees (Dahlsten, 1999; Dreistadt & Garrison, 1999). This facet of the Australian association thus appears intact; a heavy presence of lerp psyllids can cause relatively severe damage to eucalypt forests. When comparing this relationship to what naturally occurs in Australia, the next question is whether insectivorous birds function the same way in California as they do in Australia. That is, do Californian birds mediate the effects of the psyllids on eucalypt trees through predation on the psyllids?

There is anecdotal evidence that the red gum lerp psyllid is a common food item for a variety of over-wintering passerines in California (Dahlsten, 1999; pers. obs.), which suggests that an indirect effect of birds on California eucalypts is possible. Control of psyllid populations in Australia is only achieved when a diverse and abundant group of insectivores actively feed on lerp psyllids (Loyn *et al.*, 1983; Clark & Schedvin, 1999). Thus, we first look for a difference in bird diversity and abundance between an infested and a non-infested grove in California. To confirm that the birds found within the infested grove are actively feeding on the lerp psyllids, we compare foraging behaviours of the three most abundant Californian birds observed between the infested and non-infested groves, and test for a switch in foraging behaviour in the presence of psyllids. Finally, we excluded birds from portions of the infested grove to see if lerp psyllid numbers increased with the removal of bird predation.

## METHODS

A population of red gum lerp psyllids has been evident in a eucalyptus grove at Natural Bridges State Beach, Santa Cruz, California (122°3'42" W, 36°57'16" N) since the autumn of 1999. The grove is bordered on one side by suburban housing, and on the other by open scrub and grassland. Understorey vegetation is limited to some peripheral *Salix* spp. scrub. The grove itself is about 3 ha and comprises 20–30 mature trees, with canopy heights of 15–25 m. There are no canopy trees of any other genera and the surrounding topography is largely flat. In the process of conducting enclosure experiments (see below) we counted the number of lerp on a subset of leaves present in the lower canopy of the infested eucalyptus grove and estimated lerp psyllid density to be 6.2 ( $\pm$  9.4) lerp per leaf. The lerp stage was easily identifiable

by the white or sooty honeydew cap enclosing the larvae. This study site matches closely the site used by Loyn *et al.* (1983) in size (3 ha), canopy height (< 30 m), and density of lerp psyllids (estimated 2–10 lerp psyllids per leaf).

We chose a eucalyptus grove located less than three miles away at the University of California, Santa Cruz Arboretum (122°3'62" W, 36°58'93" N) as our non-infested comparison grove. This grove is similar to the infested grove in size, vegetation, topography and semiurban location, however, we did not detect lerp psyllids during the course of our study. There are many non-infested groves in Santa Cruz County, but at the time of this study there was only one infested grove. Like many efforts to measure an unexpected 'impact', we lack information on either grove before psyllid infestation. Thus, our study follows an impact-control design in which we endeavoured to reduce confounding influences on avian richness, abundance and foraging tactics (see below) by choosing a control site that is as similar as possible to the psyllid-infested site (Manly, 2001). By matching potential confounding variables (e.g. size, vegetation, topography, landscape context), we increase confidence that any differences observed in our effect variables are due to the presence of psyllids (Manly, 2001).

Our initial question is whether the infested grove supports more diverse and abundant populations of Californian birds compared to the non-infested grove. To test this possibility, we measured the species richness and abundance of birds at the infested and non-infested groves on a weekly basis between January and March 2001. This corresponds to the wet season in central coastal California and the time of year when nymph psyllids are most abundant (pers. obs.). This time frame also matches the duration of the study by Loyn *et al.* (1983), which spanned two months during the Austral wet season. We utilized point-scan techniques and counted all individuals seen or heard at points randomly selected within each grove (Bibby *et al.*, 1992). We limited count duration to 5 min in order to avoid re-sampling individuals (Bibby *et al.*, 1992). Only birds within the eucalyptus canopy were recorded.

Our second question was whether Californian birds were significantly altering their foraging patterns in order to ingest lerp psyllids when they are present. We collected foraging data for the three most abundant species — the yellow-rumped warbler (*Dendroica coronata*), Townsend's warbler (*Dendroica townsendi*) and ruby-crowned kinglet (*Regulus carendula*). We selected individual birds by walking along a set route until a foraging bird was located within the canopy of a eucalyptus tree. Moving further along the route after each focal observation reduced the probability of pseudoreplication (Lehner, 1996). We made observations no more frequently than once every five days at each site. In order to avoid preferentially recording foraging behaviours that are conspicuous and captured our attention, we began recordings after 20 s of the initial location of the focal bird (Lovette & Holmes, 1995). We followed each individual for a maximum of 10 minutes and ceased recordings when the focal individual was lost from view for more than 5 s. All observations were made between 0700 and 1500 PST and by a single observer (JJG) producing 10 h of direct observations for each species in each grove.

We recorded all foraging attack events (i.e. attempts to ingest prey) following methods described by Remesen & Robinson (1990). Classification of behaviours involved two elements; the substrate from which prey was taken (i.e. leaf, bark, twig, flower, air, sap exudates), and the type of manoeuvre involved (i.e. glean, sally, flycatch). We expect that frequency of leaf gleaning — the foraging behaviour that results in nymph or lerp covering ingestion — should significantly vary between the infested and non-infested grove if the insectivores are actively switching their foraging behaviour in response to lerp presence. Similarly, the frequency of all other foraging behaviours should decrease in the infested grove when compared to the non-infested grove.

If the lerp-infested grove is attracting a diverse and abundant group of avian insectivores and these insectivores are actively feeding on lerps, do they serve to control psyllid numbers? Loyn *et al.* (1983) and Clarke & Schedvin (1999) removed bell miner colonies in order to increase bird abundance and richness and thus induce a decrease in psyllid populations through increased predation. A tacit assumption in this argument is that the exclusion of the avian predators from portions of the psyllid infested trees (after the removal of bell miners) would allow psyllid numbers to remain high, or perhaps increase. In California, we directly tested for such an effect by creating exclusion zones that prevented access by insectivorous birds to foliage infested by nymph psyllids. We hypothesized that if bird foraging affects lerp psyllid numbers, the density of lerp psyllids would increase within the bird exclusions but would remain unchanged or decrease within areas that continued to allow access by birds.

Six bird exclusion zones were placed on *E. camaldulensis* trees selected at random in the infested grove. On each tree, we selected a shoot comprising approximately 50 leaves within the lower stratum of the canopy. We enclosed each shoot in monofilament gill netting, with a mesh size of 15 mm, which excludes birds down to hummingbird size (Sipura, 1999). This size also allows unimpeded passage of all potential insect predators. The narrow monofilament thread width of 0.2 mm avoided any visually disruptive influence and prevented birds and insects from being tangled. We visited the enclosure nets daily to remove accumulations of spider's webs that may influence predatory interactions on the shoot. Within each exclusion zone, we counted the total number of lerps on a weekly basis. Newly grown leaves were included in the counts when they reached 5 cm in length, as lerp-stage psyllids were never observed on fresh leaves below this length. A second shoot was selected on each tree to be an exclusion-free control. Control shoots comprised approximately 50 leaves, and were located in the same stratum as the exclusion zone. Lerp counts in controls were also made on a weekly basis. We compared the density of lerp-stage psyllids (in terms of mean number per leaf) inside and outside the exclusions over time using repeated measures ANOVA. All statistical analyses were performed in StatView® 5.0.

## RESULTS

The mean species richness per point count was significantly higher for the grove that harboured the red gum lerp psyllid (mean = 10.72 ± 0.76) as compared to the non-infested grove

(mean =  $7.08 \pm 0.85$ ; Mann–Whitney  $U = 136$ ,  $P < 0.05$ ,  $n = 25$ ). The mean number of individuals per point count was three times higher in the infested grove (mean =  $22.4 \pm 2.9$ ) as compared to the non-infested grove (mean =  $7.1 \pm 8.9$ ).

The three most abundant birds in our counts shifted their foraging behaviours in response to the presence of lerp psyllids. Yellow-rumped warblers had a 10 times higher rate of leaf gleaning attacks (foraging behaviour used to ingest lerps) in the infested grove (mean =  $10.18 \pm 1.13$  leaf gleans per minute) as compared to the non-infested grove (mean =  $0.24 \pm 0.076$  leaf gleans per minute, Mann–Whitney  $U = 0.5$ ,  $n = 60$ ,  $P < 0.001$ ). There was a concurrent decrease in the use of all other attacks (e.g. fly-catches, bark gleans, etc.) in the infested grove (mean =  $0.65 \pm 0.17$  for all other foraging attacks per minute) as compared to the non-infested grove (mean =  $3.73 \pm 0.55$  for all other foraging attacks per minute; Mann–Whitney  $U = 37$ ,  $n = 60$ ,  $P < 0.001$ ).

Townsend's warblers also made significantly more leaf-gleaning attacks in infested groves (mean =  $6.30 \pm 0.34$  leaf gleans per minute) compared to non-infested groves (mean =  $1.09 \pm 0.13$  leaf gleans per minute, Mann–Whitney  $U = 18$ ,  $n = 60$ ,  $P < 0.0001$ ). The same trend held for ruby-crowned kinglets (infested mean =  $9.51 \pm 0.87$  leaf gleans per minute, non-infested mean =  $2.89 \pm 0.33$  leaf gleans per minute, Mann–Whitney  $U = 48$ ,  $n = 60$ ,  $P < 0.0001$ ). Ruby-crowned kinglets also made non-leaf-gleaning attacks at a lower rate in the infested grove (mean =  $0.39 \pm 0.11$ ) as compared to the non-infested grove (mean =  $0.98 \pm 0.2$ , Mann–Whitney  $U = 291$ ,  $n = 60$ ,  $P < 0.05$ ), though there was no such difference for Townsend's warblers (infested mean =  $1.95 \pm 0.32$ , non-infested mean =  $1.92 \pm 0.34$ , Mann–Whitney  $U = 411$ ,  $n = 60$ ,  $P = 0.569$ ). Californian birds actively switched to gleaning lerp psyllids within the infested grove, and both yellow-rumped warblers and ruby-crowned kinglets decreased their use of all other foraging manoeuvres, indicating possible specialization on lerps within the infested grove.

Despite the comparatively large and diverse populations of lerp-eating insectivores within the infested grove, we found no significant difference in density of lerp psyllids inside and outside the exclusions at any point from January to March 2001 (ANOVA, repeated measures,  $F = 0.201$ ,  $n = 12$ ,  $P = 0.965$ ). Apparently the prevention of predation by birds did not have a positive effect on populations of lerp psyllids within the exclusions. Further, there was no significant difference in the rate of leaf gleaning attacks (likely to affect lerp psyllids) between birds foraging in the lower canopy (the stratum of the exclusion zones) and the upper canopy, thus indicating that our results would hold for exclusions placed higher in the canopy (data pooled for all bird predators, lower mean =  $5.24 \pm 0.57$ , upper mean =  $4.86 \pm 5.3$ , Mann–Whitney  $U = 3778$ ,  $n = 180$ ,  $P = 0.509$ ).

## DISCUSSION

We found no evidence that predation by Californian birds is currently affecting population densities of red gum lerp psyllids in a central Californian eucalyptus grove. Thus, this assemblage of birds is apparently not capable of mitigating the effects of the lerp psyllid on eucalyptus forest health. This finding contradicts

the well-studied top-down control of lerp psyllid populations by bird predators in their native Australia (once bell miners are removed) with subsequent positive effects on eucalyptus health (Loyn *et al.*, 1983; Stone, 1996; Clarke & Schedvin, 1999). This discrepancy between the bird-lerp-psyllid relationship in Australia and the one we observed in California is not due to a failure of the Californian birds to recognize and actively forage on lerp psyllids. Compared to the non-infested grove, we show that Californian passerines are present in higher numbers and greater species richness within the infested grove. Further, the two most abundant species appear to specialize on gleaning lerp psyllids in the infested grove. Neither is this discrepancy due to differences in bird abundance nor diversity between the grove we observed in California and within those observed in Australia (with bell miners removed). We observed 11 species on average within the infested grove in California. Loyn *et al.* (1983) observed 11 species within an Australian eucalypt forest once bell miners were removed. In the Australian forest, about 25 individuals were observed within infested groves once bell miners were removed. We observed a similar 22 individuals on average within the infested grove in California.

Another possible explanation for the failure of the Californian bird community we observed to control red gum lerp psyllids may lie in the short temporal and small spatial scale of contact between birds and lerp psyllids. In Santa Cruz, insectivorous birds are typically only present in eucalyptus groves from January through March. Only a few birds use eucalyptus groves as their breeding grounds and none form breeding colonies that could effectively monopolize the psyllid resource within the infested grove during the breeding season, as do bell miners in Australia. Similarly, as evinced by the presence of only one infested grove in Santa Cruz, red gum lerp psyllids in California are (currently) almost exclusively confined to small, discontinuous groves often surrounded by urban areas. This spatially limits the opportunity for birds to encounter lerp psyllid populations in Santa Cruz, and likely all of California.

However, the association between lerp psyllids and Australian birds is also temporally and spatially ephemeral. Loyn *et al.* (1983) indicated that the two groups overlap for only a few months each year. Further, the group of Australian birds that colonize bell miner-free infested groves are nomadic and thus likely encounter lerp psyllid populations relatively sporadically across their foraging range (Loyn *et al.*, 1983). This comparison suggests that the situation we observed in California is quite similar to that in Australia in terms of the timing and chances for contact between birds and nymph psyllids, and thus is an unlikely reason for the differences observed in indirect top-down effects between the two systems.

Instead, this discrepancy is most likely due to a higher rate of psyllid ingestion by Australian bird communities than was found among the birds we observed in California. Loyn *et al.* (1983) found that attack rates of 25 lerps per minute by bell miners were insufficient to have any effect on lerp psyllid populations, whilst drastic reductions in lerp psyllid populations occurred when other avian species fed at rates of 40 lerps per minute. In the infested grove in California, we observed rates of feeding

considerably lower, with a mean of seven lerps per minute calculated across all lerp gleaning species.

This difference in psyllid ingestion rates can be explained in part by a substantial difference in the body sizes, and thus energetic needs, of psyllid-eating birds in Australia as compared to those we observed in California. Loyn *et al.* (1983) report that the most common psyllid-eating birds (once bell miners were removed) were striated thornbills (*Acanthiza lineata*, 7 g), white-naped honeyeaters (*Melithoreptus lunatus*, 14 g), crimson rosellas (*Platycercus elegans*, 131 g), eastern roseallas (*P. eximius*, 111 g) and spotted pardalotes (*Pardalotus punctatus*, 9 g). The smaller birds in this group (mean body mass of 10 g) fed at rates of 25 lerps per minute, whereas the much larger roseallas (mean body mass of 121 g) fed at rates of 48 lerps per minute. The top five psyllid-eating birds we observed were yellow-rumped warblers (12.3 g), Townsend's warbler (8.8 g), ruby-crowned kinglet (6.5 g), bushtits (*Psaltriparus minimus*, 5.3 g), and golden-crowned sparrows (*Zonotrichia articapilla*, 29 g). The mean body size for all these psyllid-eaters was 12 g, which is comparable to the smaller Australian birds. However, the most voracious of these birds was the yellow-rumped warbler, which we estimated as taking 10 lerp psyllids per minute; less than half the ingestion rate of the small psyllid-eating Australian birds.

Thus, even when we account for body size differences, the birds we observed within the infested grove are not ingesting as many lerp psyllids as Australian birds. It is possible that these low attack rates are due to the relative unfamiliarity of Californian birds to both the lerp psyllids and the vegetative structure of eucalyptus groves, both of which are non-indigenous to California. However, given the evidence of a shift in foraging behaviour toward lerp gleaning within the infested grove, this unfamiliarity must be expressed in a subtle manner. In Australia there appears to be a difference between how bell miners and other birds feed on psyllids. Bell miners apparently ingest only the lerp covering and leave the nymph itself on the leaf surface (Loyn *et al.*, 1983). Other birds are more direct foragers in that they often remove the nymph and the lerp covering, or strip leaves from the trees in order to gain access to everything on the leaf (Loyn *et al.*, 1983; Clarke & Schedvin, 1999). Our methods were not capable of detecting these more subtle differences in foraging, although we did not observe leaf stripping. If Californian birds only recognize the lerp covering as a useful resource and do not ingest the nymphs, we would have been unlikely to observe significant differences in and outside the bird enclosures as the nymphs are capable of regenerating the lerp covering within 1–2 days.

The establishment and reassembly of an Australian psyllid–eucalypt–bird association within California is an example of the cosmopolitan ecology that is created through biological invasions (Soule, 1990). Such re-assemblies are becoming commonplace, with many food webs being artificially re-assembled for the purpose of biological control. Indeed, the eucalypt forests of California currently host a variety of Australian phytophage insects beyond the red gum lerp psyllid (Hanks *et al.*, 2000). In response, the state of California has sponsored the release of several Australian parasitoids that are phytophage 'natural enemies', in the hope that these efforts will control damage to eucalyptus

trees (Dahlsten, 1999; Hanks *et al.*, 2000). Several ecologists have questioned such actions (e.g. Simberloff & Stilling, 1996) on the grounds that biocontrol agents often attack native insects and thus precipitate more injury (often undocumented) than they cure. Such discussions are quite warranted, however, they fail to capture the full range of ecological issues associated with re-assembling non-indigenous food webs.

Simberloff & Von Holle (1999) suggest that facilitative interactions between multiple invaders can lead to invasional meltdowns, whereby the invasion process is accelerated and the subsequent impact on native species worsened. An alternative scenario is one where newly arrived non-indigenous species have detrimental impacts on those that preceded them (Lohrer & Whitlatch, 2002). Our results show a combination of those scenarios, whereby the presence of eucalyptus trees in California clearly facilitated the invasion of the lerp psyllid by providing an essential food resource that would otherwise be unavailable in California. However, the eucalypt–psyllid interaction is a negative one (phytophagy) that could affect the long-term persistence of eucalypt trees in California. The fate of some eucalypts in California may be especially grim if there are synergistic interactions between the lerp psyllid and other Australian phytophage insects established in California (e.g. the Australian weevil, *Gonipterus scutellatus*) or with stressful physical conditions (e.g. increasing urbanization). To our knowledge, neither of these possibilities has been explored.

For the native avifauna, the combined effect of the eucalypt–psyllid assemblage is not obviously detrimental. The psyllids appear to provide a reliable and potentially energetically rewarding food resource for over-wintering native birds within an increasingly urbanizing landscape. Such indirect linkages between native and non-indigenous components of food webs are likely more common than previously expected (Simberloff & Von Holle, 1999). Our results provide an initial example of the complexity involved when calculating the probability of establishment and level of impact of non-indigenous species, including those released as biocontrol agents. Ecologists have tended to ignore *de novo* foodwebs, such as those found in a Californian eucalypt forest, in favour of studying (relatively) intact, and native, systems. However, as we have observed here, *de novo* foodwebs are often quite complex and offer unprecedented opportunities to explore how communities are constructed (e.g. Wilkinson, 2004).

## ACKNOWLEDGEMENTS

James Gilroy completed this work while participating in a year-abroad programme sponsored by the University of East Anglia and the University of California, Santa Cruz. We thank the California State Parks and the University of California, Santa Cruz Arboretum for permission to work on their property.

## REFERENCES

- Bach, C.E. (1991) Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants (*Pluchea indica*). *Oecologia*, **87**, 233–239.

- Bibby, C.J. (1992) *Bird census techniques*. Academic Press, London.
- Bossard, C., Randall, J.M. & Hoshovsky, M.C. (2000) *Invasive plants of California's wildlands*. University of California Press, Berkeley, CA.
- Clarke, M.F. & Schedvin, N. (1999) Removal of bell miners *Manorina melanophrys* from *Eucalyptus radiata* forest and its effect on avian diversity, lerp psyllids and tree health. *Biological Conservation*, **88**, 111–120.
- Cox, G.W. (1999) *Alien species in North America and Hawaii*. Island Press, Washington, DC.
- Dahlsten, D.L. (1999) *Biological control of the red gum lerp psyllid, a pest of eucalyptus species in California*. Web resource: <http://www.cnr.berkeley.edu/biocon/dahlsten/rglp/> (last accessed November 2003).
- Dreistadt, S.H. & Garrison, R.W. (1999) *Pest notes: eucalyptus redgum lerp psyllid* (ed. by B. Ohlendorf). University of California, Department of Natural Resources Publication 7460, Davis, CA.
- Hanks, L.M., Millar, J.G., Paine, T.D. & Campbell, C.D. (2000) Classical biological control of the Australian Weevil *Gonipterus scutellatus* (Coleoptera: Curculionidae) in California. *Environmental Entomology*, **29**, 359–375.
- Hanks, L.M., Millar, J.C., Paine, T.D., Wang, Q. & Paine, E.O. (2001) Patterns of host utilization by two parasitoids (Hymenoptera: Braconidae) of the eucalyptus long-horned borer (Coleoptera: Cerambycidae). *Biological Control*, **21**, 152–159.
- Lehner, P. (1996) *Handbook of ecological methods*. Cambridge University Press, London.
- Lohrer, A.M. & Whitlatch, R.B. (2002) Interactions among aliens: apparent replacement of one exotic by another. *Ecology*, **83**, 719–732.
- Lovette, I.J. & Holmes, R.T. (1995) Foraging behaviour of American redstarts in breeding and wintering habitats: implications for relative food availability. *Condor*, **97**, 782–791.
- Loyn, R.H., Runnals, R.G., Forward, G.Y. & Tyers, J. (1983) Territorial bell miners and other birds affecting populations of insect prey. *Science*, **221**, 1411–1412.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.
- Majer, J.D., Recher, H.F., Wellington, A.B., Woinarski, J.C.Z. & Yen, A.L. (1997) Invertebrates of eucalypt formations. *Eucalypt ecology* (ed. by J.E. Williams and J.C.Z. Woinarski), pp. 278–302. Cambridge University Press, Cambridge.
- Manly, B.F.J. (2001) *Statistics for environmental science and management*. Chapman & Hall/CRC Press, Boca Raton, Florida.
- Moore, K.M. (1970) Observations on some Australian forest insects. 23. A revision of the genus *Glycaspis* (Homoptera: Lerp psyllidae) with descriptions of seventy-three new species. *Australian Zoology*, **15**, 248–297.
- Remesen, J.R. & Robinson, S.K. (1990) A classification scheme for foraging behaviour of birds in terrestrial habitats. *Studies in Avian Biology*, **13**, 144–160.
- Simberloff, D. & Stilling, P. (1996) Risks of species introduced for biological control. *Biological Conservation*, **78**, 185–192.
- Simberloff, D. & Von Holle, B. (1999) Positive interactions of non-indigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.
- Sipura, M. (1999) Tritrophic interactions: willows, herbivorous insects and insectivorous birds. *Oecologia*, **121**, 537–545.
- Soule, M.E. (1990) The onslaught of invading species, and other challenges in the coming decades. *Conservation Biology*, **4**, 233–239.
- Stone, C. (1996) The role of lerp psyllids (Hemiptera: Lerp psyllidae) and bell miners (*Manorina melanophrys*) in canopy dieback of Sydney blue gum (*Eucalyptus saligna*). *Australian Journal of Ecology*, **21**, 450–458.
- Van Driesche, J. & Van Driesche, R. (2000) *Nature out of place: biological invasions in the global age*. Island Press, Washington, DC.
- Wilkinson, D.M. (2004) The parable of Green Mountain: Ascension Island, ecosystem construction and ecological fitting. *Journal of Biogeography*, **31**, 1–4.

#### BIOSKETCHES

**Julie L. Lockwood** is an Assistant Professor within Ecology, Evolution and Natural Resources at Rutgers University. She is interested in how non-indigenous species invasions combine with native species extinctions to alter biodiversity patterns and ecological relationships.

**James Gilroy** is currently studying for a doctorate at the University of East Anglia, UK. His research is aimed at determining the conservation requirements of declining birds in agricultural landscapes. Other interests include the mechanisms and implications of long-range dispersal and vagrancy in birds.