Community-level net spillover of natural enemies from managed to natural forest

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Abstract. Edge effects in fragmented natural habitats may be exacerbated by intensive land use in the surrounding landscape. Given that most managed systems have higher primary productivity than adjacent natural systems, theory suggests that bottom-up subsidized consumers are likely to spill over from managed to natural habitats. Furthermore, the magnitude of spillover is likely to differ between generalist and specialist consumers, because of differences in their ability to use the full spectrum of resources. However, it is unknown whether there is indeed asymmetrical spillover of consumers between managed and natural habitats, and whether this is related to resource abundance or the trophic specialization of the consumer. We used flight intercept traps to measure spillover of generalist predators (*Vespula* wasps, Vespidae) and more specialist predators (106 species of parasitoids, Ichneumonidae and Braconidae) across habitat edges between native New Zealand forest and exotic plantation forest over a summer season. We found net spillover of both generalist and specialist predators from plantation to native forest, and that this was greater for generalists. To test whether natural enemy spillover from managed habitats was related to prey (caterpillar) abundance (i.e., whether it was bottom-up productivity driven, due to increased primary productivity), we conducted a large-scale herbivore reduction experiment at half of our plantation sites, by helicopter spraying caterpillar-specific insecticide over 2.5 ha per site. We monitored bidirectional natural enemy spillover and found that herbivore reduction reduced generalist but not specialist predator spillover. Trophic generalists may benefit disproportionately from high resource productivity in a habitat, and their cross-habitat spillover effects on natural food webs may be an important source of consumer pressure in mosaic landscapes.

Key words: *edge effect; generalist predator; Hymenoptera; land-sharing; land-sparing; New Zealand; parasitoid; productivity; specialist predator; spillover;* Vespula germanica; Vespula vulgaris.

INTRODUCTION

Ecosystem change due to the loss and fragmentation of natural habitats can be compounded by increased land-use intensification in surrounding habitats (Saunders et al. 1991, Fischer and Lindenmayer 2007, Tscharntke et al. 2012). An important mechanism through which this occurs is via edge effects: changes at natural habitat edges caused by high contrast in various biotic and abiotic environmental parameters between the natural fragment and the adjacent managed habitat (Murcia 1995). The level of structural contrast between habitats is an important factor determining edge effects, because it can cause dramatic microclimatic changes at the edge of a natural remnant habitat

(Didham and Lawton 1999, Cadenasso and Pickett 2000). This can subsequently cause significant shifts in species composition (Campbell et al. 2011).

High primary productivity contrast between habitats may also contribute to edge effects by determining the flow of subsidies into natural fragments (Polis et al. 1997). Subsidies generally flow from the high- to the low-productivity habitat (Oksanen 1990, Oksanen et al. 1992, Polis et al. 1997, Sears et al. 2004), where they can then influence ecosystem functioning and stability (Jefferies 2000, Huxel et al. 2002). For example, cross-boundary subsidies of nutrients generally increase productivity in recipient systems (Polis et al. 1997, Jefferies 2000, Sale and Arnould 2012, Reimchen and Fox 2013). Likewise, cross-boundary subsidies of organisms, i.e., "spillover" (Tscharntke et al. 2005, Rand et al. 2006, Macfadyen and Muller 2013), can affect trophic interactions in the recipient habitat

(Janzen 1983, 1986, Rand and Louda 2006, Chalak et al. 2010).

Globally, production land generally has higher primary productivity than natural ecosystems (Field et al. 1998). Therefore, production land likely supports higher densities of consumers than adjacent natural areas, which may lead to a general net spillover of organisms from managed habitats into adjacent natural fragments (Tscharntke et al. 2005, Rand et al. 2006). Although this may cause important changes to trophic interactions in natural habitats (Rand and Louda 2006), these effects have only recently been considered to be a potentially important mechanism causing fragmentation-related change in natural systems (Tscharntke et al. 2005, Rand et al. 2006). Consequently, they have thus far not been well studied, particularly at the community level (Blitzer et al. 2012).

Most studies of cross-edge spillover to date have focused on movement in the natural-to-managed direction, such as the movement of natural enemies (e.g., Landis et al. 2000, Sackett et al. 2009), pollinators (Garibaldi et al. 2011), plants (Cadenasso and Pickett 2001), and pest herbivores (Norris and Kogan 2000) from natural borders into agricultural systems. This spillover has been shown to substantially affect ecosystem services such as natural pest suppression and pollination (Landis et al. 2000, Klein et al. 2007, Garibaldi et al. 2011). Therefore, spillover in the opposite direction, from managed to natural systems, should also be expected to impact ecosystem functioning significantly in natural systems (Rand et al. 2006).

Primary productivity-driven consumer spillover from managed to natural habitats has been proposed for avian nest predators (Angelstam 1986), but this has mostly been speculative (Lahti 2001, 2009, Blitzer et al. 2012). Other than this, the few studies that have examined consumer spillover from managed to natural habitats (herbivores [McKone et al. 2001, Kaiser et al. 2008, Squires et al. 2009]; predators [Rand and Louda 2006, Rand and Tscharntke 2007, Gladbach et al. 2011]), as well as most studies of spillover in the natural-to-managed direction, have been carried out in agricultural landscapes. In these cases, the anthropogenic side of the edge is usually an intensively managed, fast-growing annual crop. This represents a relatively extreme case of primary productivity contrast between managed and natural habitats (e.g., a 25-fold cross-edge productivity difference [Ovington et al. 1963]), so highly asymmetrical spillover might be expected. Furthermore, temporal resource fluxes related to nutrient inputs and harvesting are also likely to cause pulsed cross-edge spillover in these systems (Ovington et al. 1963, Rand et al. 2006). It is unknown whether cross-edge spillover may be similarly important when there is a smaller cross-edge productivity difference, a relatively small structural contrast (Eycott et al. 2012), and lower-intensity management of the matrix, such as between managed plantation forest and natural forest. Furthermore, it is

unknown whether the theoretical relationship between habitat primary productivity and levels of consumer spillover between habitats is empirically detectable. This is because there are many factors in addition to primary productivity that may influence spillover and mask underlying productivity effects. These include predator behavioral responses, such as an aggregative response to high prey densities (which would drive predator movement in the opposite direction, into more productive habitats [Müller and Godfray 1997]), disturbance (Bong et al. 2013), and productivity-independent variation in habitat suitability.

Where they occur, productivity-driven spillover effects are predicted to be mediated primarily by trophic generalist, rather than specialist, predator species (Rand et al. 2006). This is for two reasons: first, because generalists are more likely to respond to complementary resources on different sides of the edge (Rand et al. 2006), to couple trophic dynamics in both habitats (Rooney et al. 2006), and therefore to have functional effects in the recipient habitat when spilling over (e.g., Squires et al. 2009). Second, it is likely that generalist predator populations can increase more in response to anthropogenic increases in productivity than can specialists (Symondson et al. 2002). This is because an increase in herbivore productivity would, for a specialist predator, mean an increase in its specific prey population. However, for a generalist predator, the increase in available resources would occur across all the various herbivore species that it can consume. Therefore, as predator trophic generality increases, so might predator population responses to productivity at a lower trophic level, but this remains to be tested.

Despite the predicted importance of spillover for generalist species, spillover of relative specialists (parasitoids) from natural to managed habitats (Landis et al. 2000, Macfadyen and Muller 2013), and in at least one case in the opposite direction (Gladbach et al. 2011), may also occur. Common to all these cases is that the same native prey species also occurred across the edge in the recipient habitat. However, this suggests that spillover of specialist predators can affect ecosystem processes in the recipient habitat, at least through changes in interaction strengths in existing parasitoid-host interactions in recipient habitats.

In this study, we used a large-scale field experiment to investigate spillover of generalist and specialist predators of lepidopteran herbivores across habitat edges between managed plantation forest and native New Zealand temperate forest. Specifically, we tested the following hypotheses: (1) There is a net spillover of both trophic generalist predators and more specialist predators (parasitoids) from managed to natural forest. (2) The ratio of individuals moving in the managed-to-natural vs. natural-to-managed direction will be higher for generalist than specialist predators, because of generalist predators' greater capacity to respond to habitat productivity. (3) The magnitude of spillover

from managed to natural forest is driven by a bottom-up, herbivore-mediated subsidy, such that when herbivore abundance is reduced experimentally, spillover will decrease.

METHODS

Study system

We conducted this study at edges between mature exotic *Pinus radiata* plantation forest and native, southern beech (Nothofagaceae)-dominated New Zealand forest in the Nelson/Marlborough region of the South Island of New Zealand (Appendix A: Fig. A1). We selected eight spatial blocks, within which we selected two sites that each comprised an edge between plantation and native forest (16 edges in total). One edge site was randomly allocated as the treatment (herbivore reduction) site, and the other site was designated as the control site within each spatial block. Blocks were at least 2.7 km apart, and sites within blocks were between 1.0 and 2.7 km apart (i.e., sites were always closest to their paired site within the block). The "edge" at each site was designated as the last row of plantation pine trees abutting the native forest, which corresponded to a clear change in understorey vegetation (see Appendix A for a description of the understorey plant composition.)

Estimated primary productivity of planted *Pinus radiata* forest in New Zealand is 18.4 Mg $CO_2 \cdot ha^{-1} \cdot yr^{-1}$ (Tate et al. 1997). This is over twice as high as primary productivity estimates for South Island New Zealand native forest: 7 Mg $CO_2 \cdot ha^{-1} \cdot yr^{-1}$ (Carswell et al. 2008) and 7.0–9.2 Mg $CO_2 \cdot ha^{-1} \cdot yr^{-1}$ (Trotter et al. 2005).

Sampling herbivore abundance and host–parasitoid interactions

To monitor herbivore abundance and host–parasitoid interactions, we sampled lepidopteran larvae both before (November 2010 and early January 2011) and after (late January and February 2011) an experimental herbivore reduction. At each of the 16 edges, we established a pair of 50-m transects parallel to the edge, with one located 10 m from the edge inside the pine plantation, and one 10 m inside the native forest. The 10 m distance was a compromise between a spatial scale over which parasitoids would be able to disperse, and a distance from the edge great enough that the vegetation was distinct from that of the adjacent habitat. We collected lepidopteran larvae from all vegetation within 1 m of either side of each transect, up to a height of 2 m, by beating the vegetation over white sheets. At 5-m intervals along each transect, we also clipped all vegetation up to a height of 9 m within a 1-m^2 area around the transect, using an extendable pole with a clipper head on the end. We beat all clippings over large sheets on the ground to collect the larvae. If canopy foliage was not accessible over the transect at the designated clipping points, we clipped four or five branches (a roughly standard number of leaves) from the closest tree that had green foliage low enough to

reach with our pruning pole. When larva collection along a transect yielded fewer than 50 individuals, we carried out additional sampling outside of the transect until we had collected 50 individuals or had sampled for up to two person-hours. These additional samples were used to supplement numbers of larvae from which to confirm host–parasitoid interactions, but were not used in the analyses of larval abundance. We reared and identified the collected lepidopteran larvae to determine what species of parasitoids attacked Lepidoptera in this system (see Appendix A for further details).

Experimental herbivore population reduction

To determine the effect of herbivore abundance on predator spillover, we experimentally reduced herbivore abundance. We sprayed the plantation side of the eight treatment (herbivore reduction) sites with Delfin WG (Certis; Columbia, Maryland, USA), an organic, non-persistent, commercial formulation of *Bacillus thuringiensis* var. *kurstaki*. This bacterial strain kills larval Lepidoptera upon ingestion, but does not affect other insects. We used a helicopter with micron air nozzles (droplet size approximately 100 μm) to spray 2.5 ha of pine plantation at each treatment site: an area 250 m along the edge, centered on the transect for lepidopteran larval collection, and 100 m toward the plantation interior from the edge. We sprayed each of the eight treatment sites twice during the southern-hemisphere summer, on 30 December 2010 and 9 January 2011, both of which were clear days with very little wind, and in most cases we observed no spray drift across the edge into the native forest. In each application, we added 4.5 kg/ha of Delfin WG, mixed with 0.125 L/ha of the wetting agent Du-Wet (Elliot Chemicals, Auckland, New Zealand). These amounts and timing were according to the manufacturers' instructions for maximal effectiveness, and comparable to amounts found to be maximally effective against lepidopteran pests (Tortricidae) in North American coniferous forests (Bauce et al. 2004).

Our herbivore reduction treatment had the desired effect (see Appendix A for an analysis of the efficacy of the herbivore reduction treatment). Herbivore abundance in treated plantation forests was reduced by 83%, whereas herbivore abundance in control plantation forests naturally increased by 58% over the same time period.

Measuring spillover of natural enemies across the edge

To compare spillover of natural enemies from plantation-to-native forest vs. native-to-plantation forest, we monitored wasp movement across the habitat edge using bidirectional malaise-style flight intercept traps (Appendix A: Fig. A2). We focused on Hymenoptera as these made up 92% of the parasitoids reared out of caterpillars. Each trap was hung from a pine tree at the edge, with its 1-m^2 collecting surface parallel to the edge. Two collecting jars on each trap separated the

capture of insects flying from the plantation vs. the native sides of the edge. We hung four traps along each of the 16 edges: two at 2 m above the ground, and two at 6–8 m above the ground (depending on the height of possible attachment points). We opened the traps in October 2010, and collected samples in November 2010 and again in early January 2011 prior to our experimental herbivore reduction treatment taking effect. For logistical reasons, the January 2011 collection actually occurred eight days after the first herbivore reduction treatment, but before the second herbivore reduction treatment. Nevertheless, we considered it to be a "before" collection, since the traps were open for at least 24 days before the first herbivore reduction treatment, and the remaining 8-day period after the first herbivore reduction treatment was not considered long enough for treatment effects to become apparent in changes in wasp movement, as it takes a few days for lepidopteran larvae to die following ingestion of the insecticide. After the two herbivore reduction treatments, we again collected trap samples in late January, February, March, and April 2011.

We lost small numbers of samples due to storm damage, which led to unequal sampling effort across sites in certain months. However, we are confident that the broken traps should not have significantly biased our treatment effects (see Appendix A for broken trap bias analysis). Nevertheless, we explicitly include sampling effort as a covariate in subsequent statistical analyses.

From the malaise samples, we removed and counted all of the Hymenoptera. Within these, we conducted further species-level sorting of natural enemy groups comprising generalist predators and more specialist predators (parasitoids). As a measure of generalist predator movement, we sorted and counted two related, non-parasitic, invasive species of social wasp *Vespula vulgaris* and *Vespula germanica* (Vespidae). We pooled these nonnative species for analysis because they are ecologically similar to the extent that *V. vulgaris*, which arrived later in New Zealand, often now displaces *V. germanica* (Beggs et al. 2011). Both species are important predators of Lepidoptera in New Zealand forests (Barr et al. 1996, Beggs and Rees 1999). As a measure of specialist predator movement, we sorted and identified the Ichneumonidae and Braconidae parasitoids. We focused on these two families because most parasitoids that we reared out of the collected lepidopteran larvae were from these families. Because our herbivore-reduction treatment focused on Lepidoptera, we excluded from our analyses any species from genera or subfamilies for which no species are known to parasitize Lepidoptera (Gauld 1984, Wahl 1993). Some parasitoid species are known to be polyphagous, and thus less specialized than others. For example, the exotic braconid *Meteorus pulchricornis* attacks 21 host species, from nine lepidopteran families in New Zealand (Berry and Walker 2004). However, as a group, parasitic Hymenoptera are more trophically specialized (Hawkins

1994) than *Vespula germanica* and *V. vulgaris*, which in the South Island of New Zealand are known to consume species from at least 21 families in nine insect orders and three arachnid orders (Harris 1991).

Statistical analysis

For all analyses of natural enemy movement, samples from the four traps at each site were pooled into single site-level samples for each forest type, to deal with large numbers of zeroes. For analysis of baseline spillover at control sites, samples were also pooled across collection dates over the entire season. For analysis of the herbivore reduction experiment, samples from control and herbivore reduction treatment sites were pooled across collection dates to create a single "before" sample and a single "after" sample at each site for each forest type within treatment, since the temporal comparison of interest was before vs. after the herbivore reduction treatment.

Baseline levels of natural enemy spillover at control sites.—To test whether there was asymmetrical spillover of natural enemies across the native–plantation edge (Hypothesis 1), we used data from the control (unsprayed) sites. We used a generalized linear mixed effects model (GLMM) with Poisson errors that included the abundance of either trapped generalist or specialist predators (in separate models) as the response, and the direction of movement (either from plantation or from native) as a fixed factor. We included site as a random factor to control for the nonindependence of edge directions within sites (i.e., each edge had movement from plantation into native and from native into plantation). We also included the number of days during which a trap was exposed, multiplied by the combined intact trap surface area at a forest type within a site (hereafter "sampling effort") as a fixed covariate to account for broken traps by removing this source of variation from the error. Here and in all subsequent analyses, the best model was selected by running the full model as well as all possible simpler models, and selecting as the final model the one with the lowest Akaike information criterion (AIC) value (Burnham and Anderson 2002). For Poisson GLMMs where overdispersion was detected (i.e., the ratio of the sum of squared Pearson residuals to residual degrees of freedom was >1.5), we included an observation-level random effect (Zuur et al. 2012), which in all cases eliminated overdispersion. All GLMMs were conducted in the lme4 package (Bates et al. 2011) for R v.2.15.0 (R Core Team 2013).

Movement ratios for generalist vs. specialist predators.—We tested whether the ratio of movement from plantation-to-native forest vs. movement from native-to-plantation forest differed for generalist vs. specialist predators (Hypothesis 2). As with Hypothesis 1, we used data from control sites, pooled across collection dates and traps. We calculated the ratio of individuals coming from plantation to individuals coming from native forest

for each predator group at each site. This movement ratio was the response variable in a Gaussian linear mixed effects model with predator group (generalist vs. specialist) and sampling effort difference between plantation and native (due to broken traps) included as fixed predictors, and site as a random factor. Assumptions of normality and homoscedasticity were violated, so we log-transformed movement ratio, after which these assumptions were met. We used a Markov chain Monte Carlo (MCMC) resampling procedure to estimate P values on the final model, as recommended by Bolker et al. (2009). The MCMC procedure was carried out using the pvals.fnc() function in the languageR package (Baayen 2010).

Natural enemy spillover in response to herbivore population reduction.—We expected natural enemies to respond to our herbivore reduction treatment primarily in the first two months following the treatment, because *Vespula* and parasitoid generation times are usually up to ~30 days (*V. vulgaris* and *V. germanica* [Leathwick 1997]; parasitoids of same genera collected in this study; e.g., Tillman and Powell [1991], Sarfraz et al. [2008]). For generalist predators, we did not have meaningful before-herbivore-reduction data because *Vespula* wasps only became abundant across sites in the month following herbivore reduction, after the new colonies that were initiated early in the summer had increased in size. Before our herbivore reduction treatment, *Vespula* wasp abundances were very low, and they were not trapped at all in 61% of sites. Therefore, we could not test for a before-after by treatment interaction (as a BACI design), but rather just compared treatment sites vs. control sites after herbivore reduction. For this we used a GLMM with Poisson errors, in which the abundance of generalist predators trapped after herbivore reduction was predicted by herbivore reduction treatment, direction of movement (out of plantation/ native) and their interaction. We included sampling effort as a fixed covariate, and site nested within block as random factors.

Parasitoids were relatively abundant both before and after herbivore reduction. Therefore, we used a GLMM with Poisson errors to test whether the abundance of specialist predators trapped was predicted by herbivore reduction treatment, direction of movement (out of plantation vs. native), collection (after vs. before treatment), and their two-way and three-way interactions. We included sampling effort as a fixed covariate, and forest type nested within site nested within block as random factors.

Our analyses of specialist predator movement included all trapped Braconidae and Ichneumonidae thought to parasitize Lepidoptera (hereafter "parasitoids"). Since the taxonomy and biology of parasitic Hymenoptera in New Zealand are poorly known, we designated individuals as either Lepidoptera parasitoids or not by using host information from the literature associated with genera or subfamilies. To ensure that this decision

did not significantly affect the results of our experiment, we reran the same analyses on specialist predator movement, but to be conservative we included only the 429 individuals of the species that we had reared out of lepidopteran larvae during our sampling (i.e., confirmed parasitoids of Lepidoptera at our sites).

RESULTS

Our trapping effort collected 1394 *Vespula* sp. wasps. We also captured 14 023 parasitic Hymenoptera, of which 1712 individuals in 106 species were Ichneumonidae and Braconidae in subfamilies or genera known to attack larval Lepidoptera. These made up our group of specialist predators. We collected 4027 (+462 in extra sampling to increase sample size of host–parasitoid interactions) larval Lepidoptera in the native forests, and of these 1320 (+132) were successfully reared through to adulthood or parasitoid emergence, generating 207 (+19) parasitoids in the families Braconidae or Ichneumonidae, as well as 30 (+8) parasitoids in other taxa.

Natural enemy levels and ratios of spillover at control sites

Significantly more generalist and specialist predator individuals moved out of plantation than out of native forest at control sites (generalists, $Z = 5.77$, $P < 0.0001$; parasitoids, $Z = 4.20$, $P < 0.0001$; Fig. 1a, Appendix B: Tables B1 and B2). On average, 88 ± 48 (mean $\pm$ SE) generalists and 66 ± 10 specialist predators per site were trapped moving from plantation to native forest over the whole season, whereas only 22 ± 13 generalists and 34 ± 3 specialist predators per site were trapped moving in the opposite direction. The ratio of the number of individuals moving from plantation to the number of individuals moving from native forest was significantly higher for generalist than specialist predators ($t = 3.09$, $P_{MCMC} = 0.0496$; Fig. 1b).

Natural enemy spillover in response to herbivore population reduction

In the model for generalist predators, there was a significant two-way interaction between herbivore reduction treatment and forest type ($Z = -5.47$, $P < 0.0001$; Fig. 1c, Table B3), with significantly fewer generalist predators coming out of plantations subject to the herbivore reduction treatment than out of control plantations, whereas there was no significant difference in the number of generalist predators coming out of native forest in the herbivore reduction vs. control treatments. This suggests that reducing the herbivore population in the plantation reduced the spillover of generalist predators from plantation to native forest. In contrast, the model of specialist predator movement across the edge revealed no significant three-way interaction between herbivore reduction, side of the edge, and collection (the interaction term was removed during model simplification; Fig. 1d, Table B4). The results from the model of specialist predator movement
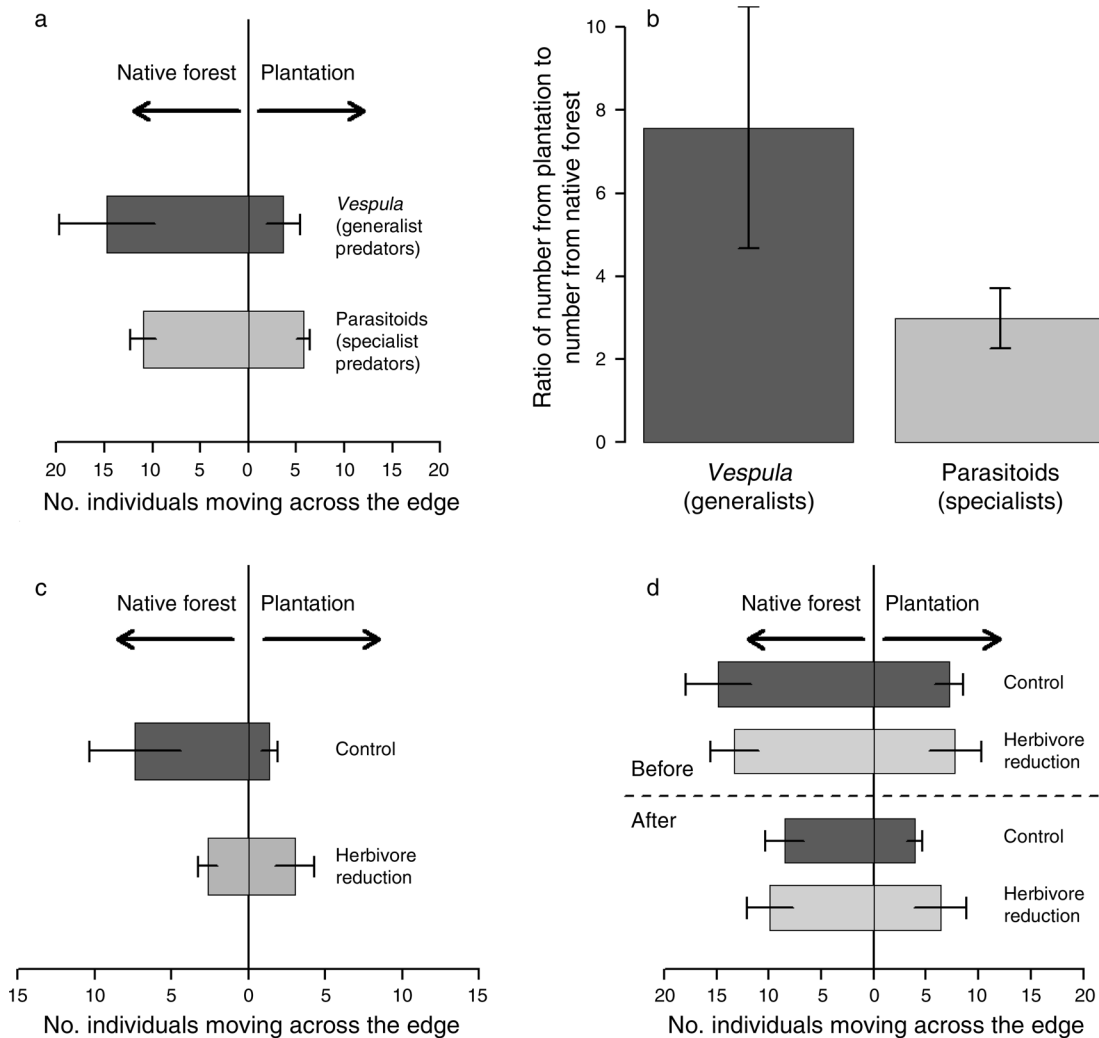
FIG. 1.   (a) Movement of generalist predators (*Vespula* wasps) and specialist predators (parasitoids) out of plantation forest into native forest, and out of native forest into plantation at control sites. The vertical line at 0 represents the habitat edge, and bars extending into native or into plantation represent number of individuals moving *into* those habitats from across the edge. (b) Ratio (mean ± SE) of the number of individuals moving from plantation-to-native forest vs. the number of individuals moving from native-to-plantation forest at control sites for generalist and specialist predators. (c) Number of generalist predators (*Vespula* wasps; mean ± SE) moving across the habitat edge from plantation to native forest and from native to plantation forest after herbivore reduction. (d) Number of specialist predators (parasitoids; mean ± SE) moving across the habitat edge from plantation to native forest and from native to plantation forest before and after experimental herbivore reduction.

including only species that were reared from sampled larvae (i.e., confirmed parasitoids of Lepidoptera at our sites) did not differ qualitatively from those obtained using the full data set (Table B5), so we do not consider them further here.

DISCUSSION

We found greater spillover of both generalist and specialist predators from plantation forest to native forest than in the opposite direction. This asymmetry supports the hypothesis that there is generally net spillover from managed to natural habitats (Tscharntke et al. 2005). Theory about asymmetrical spillover was developed with highly productive seasonal crops in mind

as the managed habitat (Tscharntke et al. 2005, Rand et al. 2006), and our results demonstrate that asymmetrical spillover can occur even along the shallower productivity gradient found between plantation vs. natural forest (Tate et al. 1997, Trotter et al. 2005, Carswell et al. 2008), and in more perennial systems that lack annual harvesting cycles.

Previously, 80% of the reported examples of managed-to-natural spillover have involved generalist species (Blitzer et al. 2012), whereas our results suggest that more specialist species may also spill over substantially. In this case, the spillover resulted in a subsidy of specialist predator abundances, rather than of novel species, into the recipient habitat, since taxonomic

composition of the parasitoids trapped moving in either direction did not differ significantly (Appendix C: Tables C1 and C2). The potential effects on recipient systems of specialist spillover warrant further attention, in particular because of the well-recognized capacity for specialists to exhibit strong numerical responses and exert strong top-down effects on prey populations (Symondson et al. 2002). In cases where a specialist predator's prey exists in the recipient habitat, it is possible that specialist predator spillover could have a stronger impact on that prey population than spillover of a generalist predator that attacked the same prey species, because of this potential for strong top-down control by specialists.

Nevertheless, the ratio of generalist predator spillover out of plantation forest relative to native forest (4:1) was significantly higher than the ratio for parasitoids (2:1). This is in line with the hypothesis that generalist predator density responds more than specialist predator density to productivity increases (Blitzer et al. 2012), because a productivity increase can multiply available resources to a greater degree for trophic generalists vs. specialists (Symondson et al. 2002). Interestingly, the ratio of net movement for parasitoids was similar to the approximately 2:1 primary productivity ratio of pine (Tate et al. 1997) to native forest (Trotter et al. 2005, Carswell et al. 2008), whereas the generalist predator ratio was twice as great. This suggests that even minor productivity differences could have important impacts in adjacent ecosystems, when bottom-up increases in multiple prey taxa are compounded by generalist predators. Furthermore, generalist predator spillover responded to herbivore abundance as predicted, in that spillover decreased significantly following experimental reduction. This supports the hypothesis that the level of generalist predator spillover depends upon herbivore productivity within a habitat (Oksanen 1990). Conversely, the lower ratio of net movement for specialist predators (i.e., their lower response to herbivore density) might explain why they did not show a detectable response to the change in herbivore abundance, and a greater herbivore reduction may have been necessary.

Greater subsidy of generalist than specialist predators by a productivity difference should cause generalists to have a greater impact than specialists on prey communities in recipient habitats (Blitzer et al. 2012). This is because generalist predators can reduce densities of more prey species, with greater flexibility to switch among prey than specialists. They should therefore be better able to engage in novel predator–prey interactions, such that even a native generalist predator, subsidized in a managed landscape (Rand et al. 2006), might form new feeding links upon spillover back into a native habitat. Generalist predator population dynamics are also less linked to prey population dynamics (Closs et al. 1999), thus making them more likely to drive prey populations to extinction in recipient habitats, particularly when they spill over into a less productive habitat

(Holt and Hochberg 2001). Spillover of generalist predators may therefore be expected to affect the structure and stability of entire food webs through both direct predation and indirect effects, such as competition, apparent competition (Holt 1977, van Veen et al. 2006), or trophic cascades (Polis et al. 1997).

In the case of the generalist *Vespula* predators considered here, resources on both sides of the edge are likely to be important (Harris 1991, Ries et al. 2004, Rand et al. 2006), such that they move back and forth across the edge from the nest location. They could thus be "ecotone species" (Duelli and Obrist 2003) that thrive at plantation–native-forest edges. In spite of this potential back-and-forth movement, we found a net movement of *Vespula* wasps into native forest. This finding may be due to the way in which experienced *Vespula* foragers navigate during flight; they tend to orient visually, relocating nests and food sources by recognizing visual cues (*V. vulgaris* [Steinmetz and Schmolz 2004]; *V. germanica* [D'Adamo and Lozada 2008]). It is only the naive foragers and foragers flying in darkness that use olfactory cues to navigate (Steinmetz and Schmolz 2004), and so it is likely that our traps caught very few experienced foragers, which would probably fly back and forth across the edge along the same routes, missing our traps on the return flight if they missed them the first time. Therefore, our traps probably caught mostly naive foragers. It is possible that *Vespula* wasp cooperative behavior and memorization of resource locations (Free 1970) means that following resource discovery, foragers focus on the largest prey resources. In this way, movement of naive foragers alone may not accurately reflect the number of prey individuals removed from each habitat, and thus *Vespula* impact on that ecosystem. However, naive forager movement should reasonably accurately reflect rates of cross-habitat resource discovery. Obviously, in nonsocial generalist predators, the directional impacts of spillover resulting from a bottom-up resource subsidy will be easier to predict.

Theoretical models predict that the impact of spillover predation on the recipient habitat should be highest when movement rates are substantial and predator attack rates on prey in the recipient habitat are high (Holt and Hochberg 2001), and both of these conditions are fulfilled here, particularly in the managed-to-natural forest direction. Empirically, the many ramifications of high attack rates by invasive *Vespula* wasps on native New Zealand southern beech forest species have been well documented (Beggs et al. 2011). In these forests, *Vespula* wasps often reach abundances high enough to affect population growth and persistence of Lepidoptera, and may even cause local extirpation of all free-living lepidopteran larvae except for those emerging in early spring (Beggs and Rees 1999). *Vespula* wasps in native forests also compete with robins for lepidopteran larvae, stealing food caches made by Robins (Barr et al. 1996), and are implicated in the declines of several

native bird species in these forests (Elliott et al. 2010). They are therefore likely to have negative indirect effects on every other predator of lepidopteran larvae as well. Finally, because lepidopteran larvae are estimated to comprise about 33% of the diet of *Vespula* wasps in this system (Harris 1991), their abundance in plantation forests likely represents a subsidy to *Vespula* that indirectly impacts other prey taxa in the native forest, although this has not been studied.

This is the first experimental study to test the hypothesis that the difference in resource abundance between managed and natural habitats drives asymmetry in community-wide cross-edge spillover (Blitzer et al. 2012), and has implications for conservation of natural fragments. A recent comparison of land-sparing strategies (keeping conservation land separate from high-production agricultural land), vs. land-sharing strategies (integrating conservation and lower-intensity production land in the same landscape) found that land sparing better maintains biodiversity at a regional scale (Phalan et al. 2011). Our results support the minimization of edge-to-interior ratios of conservation areas bordered by production landscapes, but suggest that productivity differences may exacerbate the impacts of managed areas on natural ones (Didham et al. 2012). Given that land-sparing approaches advocate the intensification of production land, our findings provide a caveat to their implementation, because increased intensification may lead to increased spillover into natural habitats. Plantation forest has been advocated as a buffer to protect natural remnants, because it is structurally more similar to natural forest than are agricultural crops (Brockerhoff et al. 2008). However, our study shows that this approach could generate spillover effects on natural forest, perhaps augmented by the structural similarity in habitat types (Campbell et al. 2011, Eycott et al. 2012) or similarity in species composition (Janzen 1983, 1986). Our results suggest that spillover of natural enemies, and the potential ecosystem-level consequences of this type of edge effect require careful consideration in the management of mosaic landscapes.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: http://dx.doi.org/10.1890/14-0696.1.sm