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Long-term consequences of invasive deer on songbird communities: Going from bad to worse?

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Abstract Although we understand many initial effects of invasive deer on songbirds, we do not yet understand how their longer-term effects unfold. We looked for such potential long-term effects on songbirds in the context of an archipelago where deer were introduced over a century ago. Initial data consist of vegetation plots and songbird point-counts on 57 islands in Haida Gwaii (British Columbia, Canada) taken in 1989 when the impacts of introduced deer lacking predators had already developed for >50 years. Twenty years later, we surveyed these islands using the same methods. To isolate the effects of deer, we compare results to nearby islands never colonized by deer and assess how canopy birds have fared relative to understory birds. We also compare responses between islands of "moderate deer impact" where the understory vegetation was only moderately depleted by deer in 1989 and those with "severe deer impact" where understory vegetation was strongly depleted even in 1989. In 1989 all islands with deer were impoverished in songbirds that depend on understory vegetation, but the moderate impact islands still had richer and more abundant understory forest-bird communities than found on severe impact islands. Islands with the fewest deer impacts in 1989 were small and isolated from sources of deer colonization. By 2009, severe deer impacts extended to islands that were initially less affected by deer. The severity of impacts also increased even on islands that had been dramatically affected by 1989. Declines in bird abundance occurred before declines in bird diversity. These results support the need for actions by wildlife managers to curtail deer impacts as soon as these become evident, especially in reserves and protected areas that lack hunters and other deer predators.

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Introduction

Invasive populations of introduced consumers such as rabbits, feral goats or deer have caused major ecosystem and community transformations (Coblentz 1978; Eldridge and Myers 2001; Simberloff et al. 2013). While we have acquired good knowledge on the nature of the transformations to be expected, there is a need to better understand the potential for and magnitude of further effects, once the most dramatic initial effects have occurred. A better knowledge of such long-term consequences of the presence of invasive herbivores or of the likelihood of achieving a new stable state becomes especially important for land managers wanting to assess ecological trajectories, particularly to evaluate the value, feasibility and consequences of large-scale controls or even eradications.

Among large herbivores, deer (family *Cervidae*) have been introduced on many island and mainland ecosystems worldwide, threatening native plant and animal communities (Dolman and Wäber 2008; Spear and Chown 2009). Similar challenges are posed in continental portions of deer native ranges as a result of the dramatic increases in many of their populations due to predator reduction and agricultural subsidies. Already in the mid twentieth century Aldo Leopold voiced alarm about the large scale ecological threat posed by growing deer populations (Leopold et al. 1947).

Today, many direct effects of invasive or expanding deer populations have been well documented worldwide (Fuller and Gill 2001; Côté et al. 2004; Dolman and Wäber 2008; Takatsuki 2009; Flueck 2010). They range from modifications in the architecture of individual plants to the functioning of ecosystems (Russell et al. 2001), and from impacts on rare plant species (e.g. Miller et al. 1992) to changes in forest regeneration and structure (e.g. Cooke and Farrell 2001; Horsley et al. 2003), understory volume and diversity (e.g. Wiegmann and Waller 2006; Perrin et al. 2011) and nutrient cycling (e.g. Wardle et al. 2001; Pastor et al. 2006). In addition to direct modification of primary production, growing evidence

demonstrates that invasive or overabundant deer also have indirect effects on animals including invertebrates (e.g. Stewart 2001; Miyashita et al. 2004), small mammals (e.g. Moser and Witmer 2000), and songbirds (e.g. Holt et al. 2011; Chollet and Martin 2013).

The impacts of deer on birds have been documented in 21 independent studies completed in temperate or boreal forests from Pennsylvania (Casey and Hein 1983; deCalesta 1994), Massachusetts (DeGraaf et al. 1991), Virginia (McShea and Rappole 2000), Wyoming (Berger et al. 2001; Anderson 2007), Haida Gwaii (former Queen Charlotte Islands, Allombert et al. 2005a, b), Gulf Islands (British Columbia, Martin et al. 2011), Alberta (Teichman et al. 2013), Anticosti Island (Quebec, Cardinal et al. 2012), Newfoundland (Rae et al. 2013), England (Perrins and Overall 2001; Gill and Fuller 2007; Holt et al. 2010, 2011, 2013), Norway (Mathisen and Skarpe 2011; Mathisen et al. 2012) and Japan (Hino 2000, 2006; Seki et al. 2014). These studies ranged from 1 year snapshots to 10 years of monitoring. The former studies compared localities varying in deer density, or islands with different histories of deer presence, while the latter focused on exclosure and enclosure designs. They dealt with a variety of deer species: white-tailed (*Odocoileus virginianus*), black-tailed (*Odocoileus hemionus*), moose (*Alces alces*), elk (*Cervus canadensis*), roe (*Capreolus capreolus*), Sika (*Cervus nippon*) and muntjac (*Muntiacus reevesi*) deer. Despite the differences in context, the results of these studies were remarkably consistent. In all situations where decades of deer introduction or overabundance had occurred, the abundance of understory songbirds was severely reduced as a result of the decline in food resources and nesting sites (Fuller 2001) that followed the dramatic reduction in understory vegetation caused by deer browsing. Increased risk of nest predation (Martin and Joron 2003) and negative effects of trampling (Gill and Fuller 2007; Wieren and Bakker 2008) have also been documented. Three recent papers have suggested that declines in songbirds attributable to invasive or overabundant deer are not just local phenomena but that they also affect the regional (Delaware, Tymkiw et al. 2013), country (England, Newson et al. 2012) or even continental scales (North America, Chollet and Martin 2013).

Although the effects of introduced or overabundant deer are well documented, the longer term temporal

dynamics of the relationship between deer and forest songbirds has been less explored. A third of the previous studies were based on exclosures (7 of 21 studies), which offer the possibility to study "restored" bird communities, or on synchronous comparison (14 of 21 studies) which provide only an indirect evaluation of effects. It remains to be evaluated whether an avian community continues to change even after decades of severe impoverishment. In particular, it is unclear whether species most sensitive to deer will continue to decline in the long-term, or rather will reach a new stable state after some decades.

We examined this alternative of long term decline versus achieving a new stable state on the remote island archipelago of Haida Gwaii where Sitka black-tailed deer *Odocoileus hemionus* were introduced at the end of the nineteenth century. On the southern islands, where this study took place, uncontrolled deer populations have been present at least since the first half of the twentieth century (Golumbia et al. 2008). They severely affected tree and shrub regeneration (Martin and Baltzinger 2002; Stroh et al. 2008), simplified understory vegetation structure and diversity (Stockton et al. 2005; Chollet et al. 2013) and impoverished understory insect and songbird communities (Allombert et al. 2005a, b).

Methods

Study area and deer impact

The Haida Gwaii archipelago (formerly Queen Charlotte Islands) comprises 350 islands and islets situated between 50 and 130 km off the north coast of British Columbia (Pojar 2008). There are two large islands, Graham in the north and Moresby in the south. The southern half of Moresby Island and adjacent smaller islands, where most of our study islands were located (Fig. 1), were incorporated into the Gwaii Haanas National Park Reserve and Haida Heritage Site (hereafter Gwaii Haanas) in 1993. The climate is cool temperate, oceanic, humid-perhumid (Pojar 2008). The mean annual precipitation on the east coast is 1,400 mm (Sandspit station, Environment Canada). The landscape of the study islands is dominated by closed canopy coniferous forests of western hemlock

Tsuga heterophylla, western red cedar *Thuja plicata*, and Sitka spruce *Picea sitchensis* (Pojar 2008).

As is the case on many remote islands, native biodiversity on Haida Gwaii is impoverished when compared to the mainland. Since the late eighteenth century, about 170 plant species and ten species of mammals have been voluntarily or involuntarily introduced to Haida Gwaii (Golumbia et al. 2008). Among them, the black-tailed deer (*Odocoileus hemionus sitkensis*) is the most widespread introduced vertebrate. There were no ungulates present on the archipelago except for a small localized and relict population of caribou that became extinct at about the time of deer introduction (Byun et al. 2002). Deer colonized most islands in the archipelago and quickly reached high densities in the absence of significant predators (~ 20 deer/km^2 on average, Martin and Baltzinger 2002).

Although island size and isolation influence the local vegetation (e.g. Sitka spruce is dominant on the smaller islands, western hemlock on the larger), previous studies identified the presence or absence of black-tailed deer as the overriding force currently shaping these forest plant and animal communities. Synchronous comparisons among islands with and without deer have demonstrated that deer presence had dramatically simplified understory vegetation structure and diversity (Stockton et al. 2005; Gaston et al. 2006; Chollet et al. 2013). Vegetation studies have shown that understory vegetation cover was typically lower than 20 % on islands with a browsing history that exceeded 50 years. It ranged between 35 and 60 % on islands that have had deer present for less than 20 years (see Vila et al. 2004). Understory vegetation cover exceeded 75 % on all islands without deer (Stockton et al. 2005; Martin et al. 2010; Chollet et al. 2013). Lower vegetation cover correlated to a similar level of impoverishment in understory insects and songbirds (Allombert et al. 2005a, b). While soil type and depth or exposure had an effect on local vegetation composition, the amount of understory vegetation cover was clearly driven by presence or absence of deer.

Because islands lacking deer were among the most isolated, the impact of deer resulted in local biogeographic patterns opposite to those expected from classical island biogeography. Thus, in contrast to the usual situation, biodiversity was highest on the smallest and most remote islands. Bryophytes were the only exception to this trend, with higher local

Fig. 1 Location and map of study area. *Numbered* islands refer to the 47 islands of the main data set that are listed in Online Resource 1 (number = id in Online Resource 1). They were sampled in 1989 and 1991 (period T1) and in 2008–2009 (period T2). The small islands with spelled out names refer to the ten islands of the second data set. They were sampled in 1989, 1999 and 2007. The four islands never colonized by deer were Low Island, Lost Island, South Low and Tar islands, the four islands colonized for less than 20 years at the outset of study were North, West, South and East Skedans Islands and the two islands that have had deer for over 50 years at the outset of study were West Limestone and Haswell Island
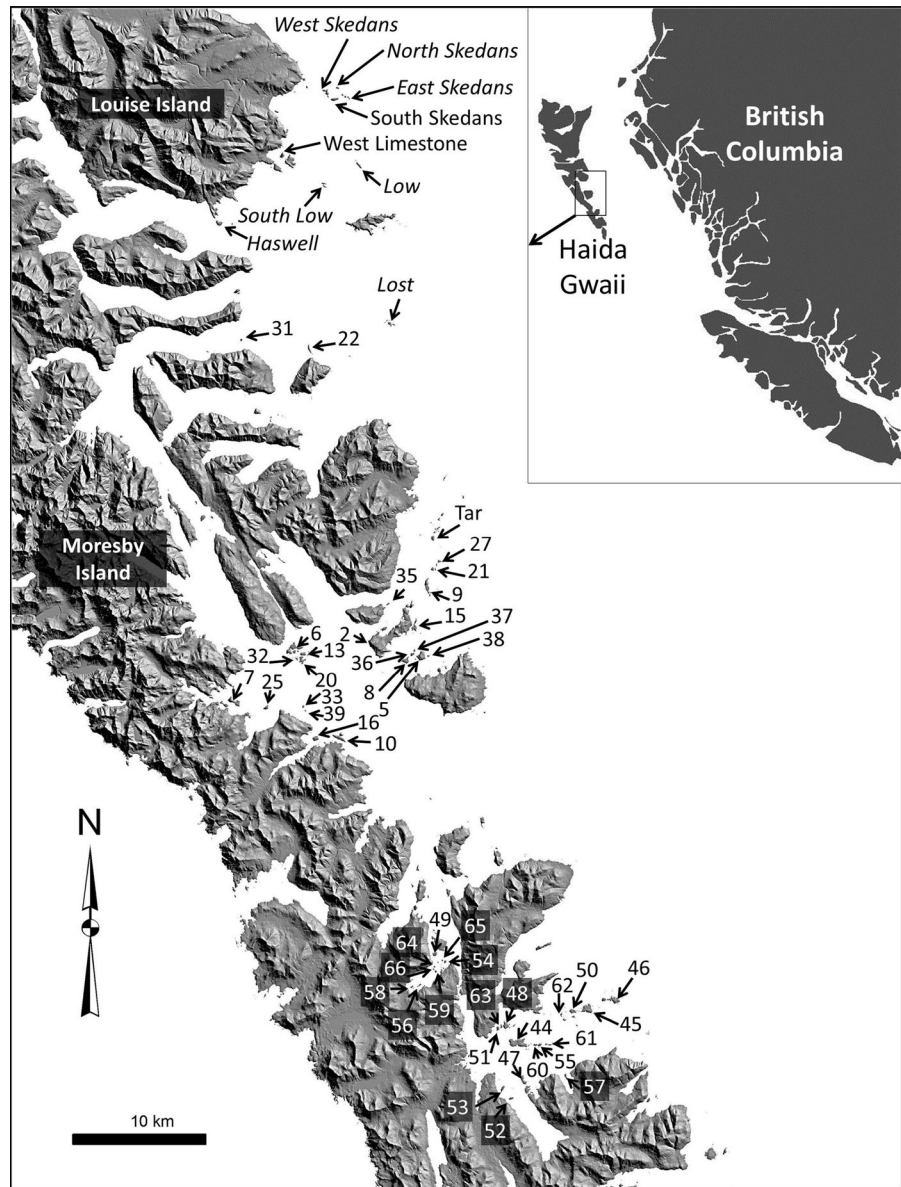
species richness and abundance on the islands most severely affected by deer (Chollet et al. 2014).

Study design

To address the question of continuous decline versus new stable state, we used data collected over a 20 year period on a set of 47 islands with deer. To minimize the risk to misinterpret values obtained at two points in time as evidence of ongoing erosion in songbird populations, we used a second dataset collected at three points in time during the same 20 years on ten additional islands (islands with spelled out names on Fig. 1). This second set of islands included three islands never colonized by deer (see Fig. 1) which served as a reference for the state of the bird community in the absence of deer, four island that, in 1989 at the outset of the study, had been colonized for less than 20 years (Vila et al. 2004) and three islands that had had deer for at least 50 years.

In both analyses we used canopy birds, a guild we considered unlikely to be affected by deer browsing

Table 1 Species dependence on understory vegetation (after Allombert et al. 2005b)

Species name	Foraging	Nesting	Dependence score
Rufous hummingbird *Selasphorus rufus*	3	1	4
Orange-crowned warbler *Vermivora celata*	2	2	4
Pacific wren *Troglodytes troglodytes*	2	1	3
Fox sparrow *Passerella iliaca*	1	2	3
Song sparrow *Melospiza melodia*	1	2	3
Swainson's thrush *Catharus ustulatus*	1	2	3
Hermit thrush *Catharus guttatus*	1	1	2
Varied thrush *Ixoreus naevius*	1	1	2
Golden-crowned kinglet *Regulus satrapa*	1	0	1
Pacific Slope flycatcher *Empidonax difficilis*	0	1	1
Brown creeper *Certhia americana*	0	0	0
Chestnut-backed chickadee *Parus rufescens*	0	0	0
Hairy woodpecker *Picoides villosus*	0	0	0
Red-breasted sapsucker *Sphyrapicus ruber*	0	0	0
Townsend's warbler *Dendroica townsendi*	0	0	0

We considered species with scores of 2 or more as dependent on understory vegetation and species with scores of 1 or 0 as not dependent on understory vegetation

(e.g. Allombert et al. 2005a, b; Chollet and Martin 2013), as a control for the study of the expected effects of deer on understory birds.

Temporal and spatial extent of surveys, island area and isolation

The 47 islands of the first data set were distributed along a 60 km north–south axis along the east side of Haida Gwaii. We measured their vegetation cover and censused their songbird communities between 1989 and 1991 (time period T1) and again in 2008 and 2009 (period T2) (Table 1; Fig. 1). These islands varied in size from 1 to 425 ha (mean 19.2 ha) and deer were present on all of them. They were separated from the closest larger islands (>500 ha), their likely source of deer colonization, by distances varying from 50 to 3150 m (mean 1,054 m). Dates of the first colonization by deer are not known for each island but records of deer as far back as 1946 at the southern tip of the archipelago (Golumbia et al. 2008) and dendro-ecological studies by Vila et al. (2004) suggested that at the outset of this study deer had been present for 50 years or more on all of the most accessible islands.

The ten islands of the second dataset were situated in the northern section of the study area (see Fig. 1). The four islands that had never been colonized by deer ranged from 9.6 to 4.5 ha in area and were all further than 2300 m from any larger island. The four islands that had been colonized less than 20 years before this study, ranged from 8.2 to 1.7 ha in area and were at 1,600–1,700 m from the larger islands. Finally, the two islands that had been colonized at least 50 years before were 16 and 13.3 ha in area and laid at less than 300 m from any larger island.

Data on forest birds and vegetation

We measured forest songbird species richness and abundance and described the vegetation with the methods used by Martin et al. (1995). We surveyed birds by means of 50 m radius, 20 min point-counts (Bibby et al. 1992) during the breeding period (mid-May to mid-June), exclusively in the morning before 11 a.m., and under uniform weather conditions (absence of steady rain and wind less than three on Beaufort scale). Drizzle and light breeze were tolerated as they did not have any noticeable effect on bird activity in the forest. All of the surveys were carried in mature forests below 150 m asl. On the 47 islands of the main data set we surveyed 88 point-count stations at T1 (the 1989–1991 period) and resurveyed them at T2 (the 2008–2009 period) (details of point-count numbers per islands are provided in Online Resource 1). The time interval between the two surveys for a given point-count varied between 17 and 20 years. We ensured that all point-counts were made at a similar distance from the shore, irrespective of island size to control for biases due to edge-effect. This distance was never less than 50 m and rarely exceeded 150 m. To

ensure independence of observations from different survey-points, we left at least 200 m between adjacent points. On the smallest islands these rules restricted the number of possible survey-points. On each island, the possible survey-points were distributed so as to be uniformly spread over the area considered. The location of each point at T1 was recorded on topographic maps and later incorporated into a Geographic Information System when the technology became available. This allowed us to locate the point-counts carried out at T2 very close to those used at T1.

We randomized visits to the islands to avoid systematic variation in survey conditions associated with island area or island isolation. For all point-counts, we recorded all bird species heard or seen as well as the number of individuals identified per species within the 50 m radius of the survey-point ($\sim$0.8 ha around the observer), during a period of 20 min. The 50 m radius was used to reduce observer errors and biases that are known to increase with distance from the point-count center (Bibby et al. 1992). During T2 a laser range finder was used to more accurately estimate distance. Each survey-point was sampled only once within each sampling period (T1 and T2). During a continuous 20 min period, it is difficult for an observer to assess if songs heard minutes apart represent one or several individuals. This difficulty is reduced by splitting the 20 min into four 5 min subsamples (Bibby et al. 1992). We therefore divided point-counts of 20 min into four 5 min sections in order to get a more accurate estimate of local abundance for a given bird species and selected the highest number of different individuals identified in a single 5 min subsample as the abundance estimate. We followed MacKenzie et al. (2002) and used these 5 min sub-samples to verify the absence of statistically significant biases in bird detectability and concurred with Gonzalo-Turpin et al. (2008) that 50 m radius 20 min point-counts were not significantly sensitive to sampling artifacts and detectability biases in contrast to shorter point-counts.

We followed the same survey methodology for songbirds on the smaller set of ten islands surveyed in 1989, 1999 and 2007. The total number of bird census plots established in each of the three island categories (without deer, with deer for less than 20 years and deer for over 50 years at outset of study) varied between four and seven. To compensate for the limited number of independent plots that can be established on any of

these small island most points were surveyed four times per season and their scores averaged out.

At each survey-point we recorded a standardized description of the understory vegetation (<4 m) structure and cover within a 25 m radius centered on the plot. We estimated the average percentage cover in the plot of the dominant plant species in the understory (>1 %) by strata (0–0.25, 0.25–0.50, 0.50–1, 1–2, 2–4 m). To estimate percentages of cover we used standard spot-charts (Mueller-Dombois and Ellenberg 1974). The charts provided patterns of black patches corresponding to patch covers of 1, 5, 10, 20 etc. up to 90 % respectively. In the plots with dense and diverse vegetation the observer had to move around the plot. In plots with an open understory or uniform vegetation (e.g. conifer regeneration) estimates were done from the center of the plot. We summed estimates of percentage cover of all understory species, including regenerating trees in the strata below 4 m, to obtain a variable that represented understory vegetation density and compared its variation between the two periods.

Assessing deer densities

Deer densities were not documented for each of the islands studied. However systematic surveys based on deer visual counts, deer pellet sampling and deer cull programs, on several small and medium-sized islands of the archipelago (Daufresne and Martin 1997; Stockton et al. 2005; unpublished data) yielded density estimates that were of similar magnitude across islands. They ranged from 21 to 37 deer/km^2 and were independent of the time since deer colonization. In the course of this study, projects were run on these islands on an almost yearly basis since 1999 and we documented no evidence of dramatic year to year fluctuations in deer presence. A recent study (Le Saout et al. 2014) based on marked and GPS collared deer on three different islands provided strong evidence that even on small islands (less than 50 ha) close to larger islands deer remained on the islands year round, commuting among adjacent islands only rarely.

Data analysis

Defining island deer impact categories

To fulfill our objective to examine the changes that occurred in bird communities on islands with deer

during the 20 year period covered by our study, we used the evidence provided by the former studies to group the 47 islands of the first dataset according to their relative deer impact (assessed via understory vegetation cover) at the outset of the study. To be conservative, we classified islands in two broad groups. We considered islands with deer and with >20 % cover of understory vegetation at T1 as moderately affected by deer ("moderate impact"), whereas we considered those with <20 % cover as severely affected ("severe impact"). It should be noted that the use of other cut-off thresholds (15, 25 or 30 %) would not have significantly changed the distribution of islands among the two groups.

We used the second set of ten islands to qualitatively assess if our results collected at two points in time were likely to reflect a regular temporal trend.

Defining bird guilds

We excluded raptors (four species) and corvids (two species) from all analyses. We also excluded pine siskin (*Carduelis pinus*) and red crossbill (*Loxia curvirostra*) from the abundance analysis because they occurred in flocks that prevent proper abundance estimates by the point-count survey method (Bibby et al. 1992). Finally, because such samples are statistically insignificant, we excluded species that were recorded fewer than five times across all surveys.

We defined bird guilds by grouping bird species in relation to their dependence on understory vegetation for foraging and/or nesting, following Allombert et al. (2005b). For this we used the literature especially as it applied to British Columbia and the Pacific Northwest (Godfrey 1986) and our own observations, to score the expected dependence of each bird species on understory vegetation for nesting and foraging (Table 1). We assigned a score between zero (no use of understory vegetation) and three (exclusive use of understory vegetation) independently for both nesting and foraging. We gave equal weight to the two scores and summed them to yield an overall score of bird species dependence on understory vegetation. We then split birds into two groups: species with marked dependence on understory vegetation (total score of two or above), and species with no dependence on understory vegetation (total score of 1 or 0, see

Table 1). We used the latter as a control assumed to be independent of deer impact.

Statistical analysis

We used two variables to study changes in the bird community: species richness, measured as the total number of songbird species detected during a point-count, and species abundance, defined as the highest number of distinct individuals recorded in a 5-min period. We transformed bird total abundance and species richness data by a $\log(y + 1)$ function.

In the analysis of the main data set of 47 islands we first used the initial survey (T1: 1989–1991) to analyze the link between island characteristics (isolation and area) and songbird distribution. Second, we analyzed the changes in vegetation and bird species richness and abundance observed between T1 and T2 (2008–2009) for the entire set of islands. Finally, we analyzed the changes between T1 and T2 in bird communities for each of the two island categories we had defined according to deer impact as observed at T1. In each instance we used a generalized linear mixed model procedure (Pinheiro et al. 2009), with normal error structure. We used "Isolation", "Area", "Time period" and "Island category" as class explanatory variables (fixed effects). To integrate possible variation resulting from among-island differences, we used islands as a random explanatory variable (random effect) but without testing for their effect. We analyzed changes in bird species richness and abundance for each group of species relative to its dependence on understory vegetation. For all statistical procedures we used R software version 2. 12 (R Development Core Team, 2011).

Results

Temporal changes in the 47 island data set

At the outset of the study, 25 islands of the 47 island dataset had an understory vegetation cover greater than 20 %, indicative of moderate deer impact. Their average understory vegetation cover was 70 % (SD = 4.6) and their area ranged from 1 to 27 ha (median area = 3 ha, Online Resource 1). The 22 remaining islands had an understory vegetation cover of less than 20 % at the

Table 2 Linear mixed models among bird species richness and abundance at T1 (1989 and 1991) in relation to island isolation and area

	Variable	DF	t value	p value
Understory independent birds				
Species richness	Isolation	44	−0.50	0.61
	Area	44	1.83	0.07 (*)
Abundance	Isolation	44	−0.44	0.65
	Area	44	1.76	0.08 (*)
Understory dependent birds				
Species richness	Isolation	44	2.64	0.01**
	Area	44	−1.18	0.24
Abundance	Isolation	44	2.63	0.01**
	Area	44	−1.69	0.09 (*)

"Island" is included in the models as a random effect and is not tested. *DF* degree of freedom and (*) $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

outset of the study, indicative of more severe deer browsing. Their average vegetation cover was 16 % (SD = 3.8) and their area ranged from 1 to 425 ha (median area = 7.3 ha, Online Resource 1) and. These two groups of islands did not differ in average isolation from the main islands (1,111 and 989 m respectively, Online Resource 1).

Characteristics of forest bird communities at T1 in relation to island isolation and area

At T1 (1989–1991), the richness and abundance of birds that depended on the understory vegetation on the 47 islands of the main data set were positively correlated with island isolation (Table 2). There was no significant correlation between island area and species richness for that guild, but there was a marginally significant negative correlation between island area and species abundance (Table 2). Thus, at the outset of the study, the more isolated an island, the richer and more abundant the understory-dependent birds recorded in a survey-plot.

For species with no dependence on the understory vegetation, we observed a weak positive relationship between island area and species richness or abundance at the outset of the study suggesting that these species tended to be relatively more abundant in survey-plots on larger islands (Table 2).

Changes in vegetation cover and bird communities between T1 and T2

There was a dramatic reduction in understory vegetation cover between T1 and T2 on both moderate (−60 % cover) and severe (−72 % cover) deer impact islands (Table 3). In addition our results indicate a strong interaction effect between "time" and "island category" (Table 3).

In both categories of islands the richness of understory-dependent bird species, although lower at T2, did not differ significantly between periods (Fig. 2; Table 4). However, their abundance was significantly lower at T2 than at T1 for both island categories ("severe" −21 %, "moderate" −17 %, Fig. 2; Table 4). There were no significant interactions between "time" and "island category" for either species richness or abundance for these understory-dependent species (Table 4).

Bird species richness of our control group (birds not dependent on understory vegetation), was lower at T2 in the category of severely impacted islands (−15 %) but was higher in the category of moderate impact islands (+42 %, Fig. 2; Table 5). Their abundance did not change during the study period on severe impact islands, but increased significantly on moderate impact islands (+64 %, Fig. 2; Table 5). For this group we found a strong interaction between "time" and "island category" for both species richness and abundance (Table 5).

Temporal changes in the ten islands data set

Among the set of ten islands for which we had data for three points in time (Fig. 3) the species richness and abundance of understory-dependent birds were highest on the islands without deer for which they remained similar in all three temporal surveys (Fig. 3). Bird species richness and abundance on the islands more recently colonized by deer were high at the outset of the study with a marginal trend of decrease over time. On islands with deer for more than 50 years in 1989 species richness and abundance of the understory-dependent species was dramatically lower than on the islands known to have been colonized less than 20 years before and values were lowest in 1999 and 2007.

Species richness and abundance of our control species group not dependent on the understory

Table 3 Variation in mean vegetation cover (with their standard deviation) between the initial study period T1 (1989 and 1991) and second study period T2 (2008–2009)

Impact at outset	T1	T2	Change	DF	t value	p value
Severe	16.36 (3.88)	4.48 (2.59)	↘	70	3.87	$p < 0.01$**
Moderate	70.2 (4.61)	41.7 (6.87)	↘	50	5.11	$p < 0.001$**
Period × Island category				120	−3.2	$p < 0.001$***

Significance of differences between T1 and T2 and interaction time/island category ("Severe impact", "moderate impact") were tested by linear mixed models with "Island" as a random factor (not tested). Arrows indicate direction of change (increase, decrease or none). *DF* degree of freedom and * $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$
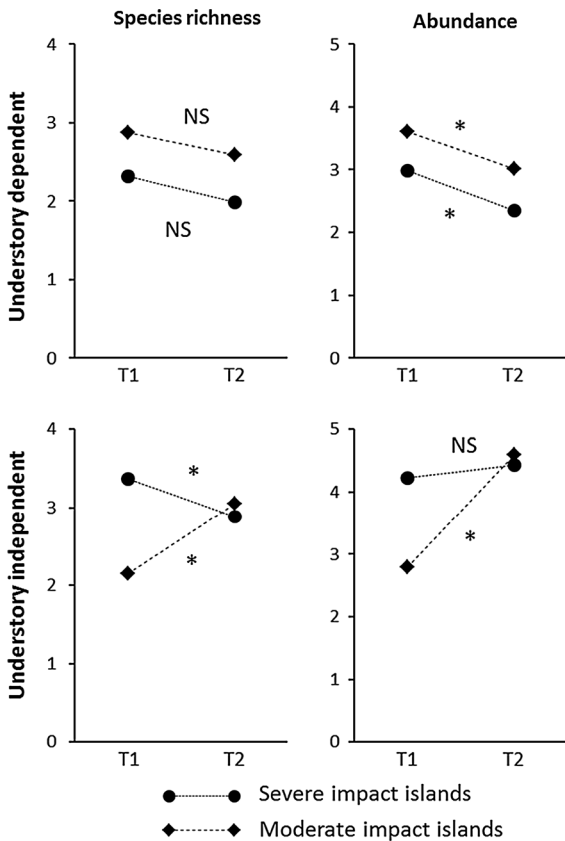

Fig. 2 Variation in mean species richness (*left*) and abundance (*right*) of understory dependent (*top*) and understory independent bird (*bottom*) for the main data set of 47 islands between the initial study period T1 (1989–1991) and second study period T2 (2008–2009). Islands were divided into two groups. Those with severe deer impact in the understory at the outset of the study and those with moderate impact at the outset of the study. Significance of change throughout time is given by stars and refers to models detailed in Tables 4 and 5

fluctuated from one year to another across the islands with a general trend of higher abundance at the end of the study period (Fig. 3).

Discussion

An overall trend of continuous erosion in understory songbirds

Our comparison of vegetation cover and bird communities twenty years apart suggest that the negative effects of deer on vegetation and songbirds, identified in 1989 (T1) through a comparison with bird communities on islands without deer (Martin et al. 1995; Allombert et al. 2005a, b), had become more severe by 2009 (T2). Songbird data collected in 1989, 1999 and 2007 in the additional set of ten small islands among which four were never colonized by deer (Fig. 3), although based on a smaller data set, were consistent with this conclusion in the sense that the differences we observed between the start and end of the study reflected an overall temporal trend of erosion in the local abundance and species richness of understory songbirds.

A temporary delay in severity of impact among islands

The existence of islands with moderate or severe deer impact in 1989 presumably resulted from the relative attractiveness and accessibility of the islands to deer. Island isolation could hinder deer immigration from the larger islands (>500 ha), the likely source of colonization, while island area could limit population persistence. Our results indicate that island isolation was likely more important than area in explaining the variation in impact we documented in 1989. More remote islands supported the highest species richness of understory-dependent species. Delays in deer colonization have actually been documented for small, isolated islands on Haida Gwaii by Vila et al. (2004) and the link between delayed colonization and lower

Table 4 Variation in mean species richness and abundance of understory dependent birds (with their standard deviation) between the outset of the study T1 (1989 and 1991) and the second study period T2 (2008–2009)

Impact at outset	T1	T2	Change	DF	t value	p value
Severe						
Species richness	2.31 (0.17)	1.98 (0.14)	–	50	1.31	NS
Abundance	2.98 (0.24)	2.35 (0.16)	↘	50	1.88	$p < 0.05$*
Moderate						
Species richness	2.87 (0.2)	2.59 (0.24)	–	50	1.29	NS
Abundance	3.61 (0.27)	3.02 (0.34)	↘	50	2.05	$p < 0.05$*
Period × Island category						
Species richness				120	0.6	NS
Abundance				120	−0.28	NS

Significance of differences between T1 and T2 and interaction time/island category ("severe impact", "moderate impact") were tested by linear mixed models with "Island" as a random factor (not tested). Arrows indicate direction of change (increase, decrease or none). *DF* degree of freedom and * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 5 Variation in mean species richness and abundance of understory independent birds (with their standard deviation) between the initial study period T1 (1989 and 1991) and second study period T2 (2008–2009)

Impact at outset	T1	T2	Change	DF	t value	p value
Severe						
Species richness	3.37 (0.15)	2.88 (0.17)	↘	70	2.22	$p < 0.05$*
Abundance	4.23 (0.21)	4.43 (0.31)	–	70	0.15	NS
Moderate						
Species richness	2.15 (0.19)	3.05 (0.25)	↗	70	−3.04	$p < 0.01$**
Abundance	2.79 (0.27)	4.59 (0.44)	↗	70	−3.39	$p < 0.001$***
Period × Island category						
Species richness				120	3.62	$p < 0.001$***
Abundance				120	3.12	$p < 0.01$**

Significance of differences between T1 and T2 and interaction time/island category ("Severe impact", "moderate impact") were tested by linear mixed models with "Island" as a random factor (not tested). Arrows indicate direction of change (increase, decrease or none). *DF* degree of freedom and * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

depletion of the understory vegetation was demonstrated by Stockton et al. (2005). The correlation between a given level of depletion in understory vegetation by deer and the level of reduction in abundance of songbirds that depend on the understory has been shown by Allombert et al. (2005a, b) and further emphasized by Martin et al. (2013). What we showed here is that the mitigating effect of island isolation on the degree of deer impact on plant and bird communities waned over time. After 20 years, the most isolated islands accessible to deer showed significant reduction in understory vegetation cover and understory dependent birds. But the changes we observed in understory-dependent birds on the "moderate impact" islands were significant only for bird

abundance. The lack of a significant effect on species richness may simply result from insufficient power to detect a change. It could also partly reflect the fact that a progressive reduction in the local abundance of a species has to reach a certain threshold before it affects the number of species actually recorded in a sample.

An absence of evidence of a new stable state

The most sobering result of our study is the reduction in the abundance of understory songbirds on the 22 islands that were already severely impoverished at the beginning of the study. At T1 these islands already exhibited a very low cover of understory vegetation and a much reduced understory bird fauna. But this did
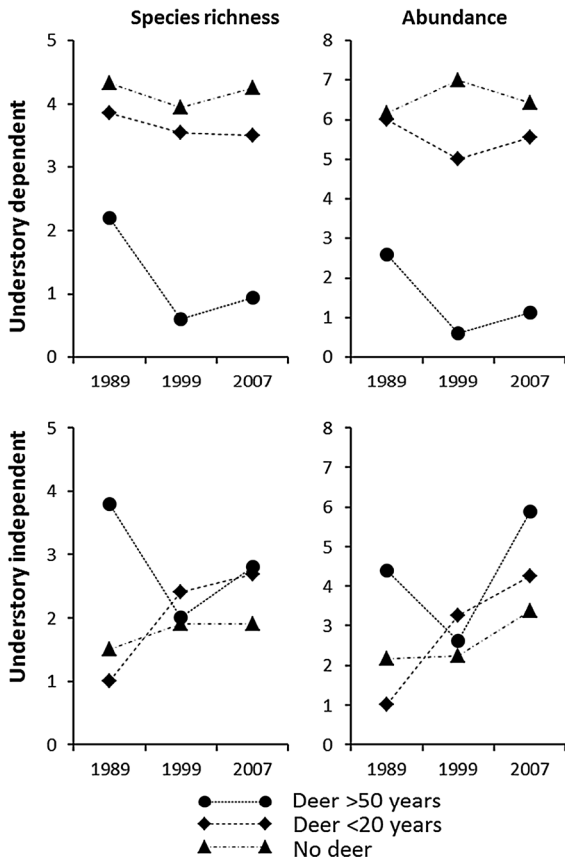
Fig. 3 Variation in mean species richness (*left*) and abundance (*right*) of understory dependent (*top*) and understory independent birds (*bottom*) for the set of ten islands of the second data set. Islands were separated into three categories relative to time since deer colonization (islands that never had deer, four islands; <20 years of deer presence at outset of study, four islands; >50 years of deer presence at outset of study, two islands). Islands were sampled in 1989, 1999 and 2007. Sample sizes per island category varied from 4 to 7 point-counts/year

not prevent further losses. Our results show that, despite the presence of deer for more than 50 years on these islands, and whatever the level of impact this had led to at the outset of this study, both plant and songbird populations had continued to decline between 1989 and 2009 with no evidence of a new stable state having been reached.

Non-understory dependent birds may not be true long term controls

The gains in richness in non-understory birds we observed over time on islands with moderate deer impact at the outset could tentatively be interpreted as a positive effect of the reduction in vegetation cover on foraging opportunities for insect feeder such as pacific slope flycatcher (*Empidonax difficilis*) or, more generally, reflect a release from competition from birds that depend on the understory. However, the decrease in local species richness for these songbirds that do not depend on the understory, and their lack of abundance gain at T2 on the "severe impact" islands, contrary to islands with moderate impact, suggest a long term impact even on the species of that group. These speculations contradict our assumption that songbirds not dependent on the understory can serve as a control against which to compare the effects of deer on understory-dependent species. They need to be tested and the possibility that, in the longer term, even songbirds that do not depend on the understory vegetation may ultimately suffer because of a decline of canopy insects, especially of those insects which spend part of their life in the understory, would deserve further investigation.

The challenges posed to conservation by "laisser faire"

Our results emphasize the extent of the challenge posed to the long term ecological integrity of the protected area of Gwaii Haanas (AMB 2003) and, at a broader geographic scale, suggest that in the absence of other mechanisms of deer population control (hunting, predators, extreme weather events) deer populations may continue to increase their impact over the long-term even where they have already caused a drastic reduction in understory vegetation and in understory-associated birds. In a context of expanding deer populations in large parts of North America, Europe, New Zealand and Japan our results could have continent-wide implications (e.g. see Chollet and Martin 2013) and should be considered carefully when it comes to the long-term management of vegetation and bird diversity, especially in forest reserves and protected areas (Underwood and Porter 1997; Porter and Underwood 1999) where hunting is prohibited and where key predators of deer are missing.

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