1   **Divergent effects of forest edges on host distribution and seed**

2   **disperser activity influence mistletoe distribution and recruitment**

3   **Running title: Mistletoe response to forest edges shaped by host and disperser.**

4   Ainhoa Magrach [1,2]*, Javier Rodríguez-Pérez [3,4], Martín Piazzon [5], Luis Santamaría [5,6]

5   [1] Institute of Terrestrial Ecosystems, ETH Zürich, CHN G 73.1 Universitätstrasse 16, 8092

6   Zürich, Switzerland

7   [2] Centre for Tropical Environmental and Sustainability Science (TESS) and School of Marine

8   and Tropical Biology, James Cook University, Cairns, Queensland 4878, Australia.

9   [3] UFZ Helmholtz Centre for Environmental Research – Umweltforschungszentrum, Dep. of

10   Ecological Modeling, PF 500136, DE-04301 Leipzig, Germany

11   [4] Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, and Unidad

12   Mixta de Investigación en Biodiversidad (UMIB, CSIC-Uo-PA), E-33071 Oviedo, Spain

13   [5] Mediterranean Institute for Advanced Studies (IMEDEA, CSIC-UIB), C/ Miquel Marquès

14   21, E07190 Esporles, Mallorca, Balearic Islands, Spain

15   6 Doñana Biological Station (EBD-CSIC), C/ Americo Vespucio s/n, E41092 Isla de la

16   cartuja, Sevilla, Spain.

17   * Correspondence author. E-mail: ainhoa.magrach@usys.ethz.ch

18   .

19

20   1. **Summary:** Species interactions define functional diversity and community stability

21   across ecosystems, and depend on the spatial distribution, the habitat requirements,

22   and the sensitivity to disturbances of all interacting partners. Hence, assessing the

23   effects of such anthropogenic disturbances on multi-species interactions may be

24   essential to improve adaptation and mitigation measures for biodiversity conservation.

25   2. We determined the importance of edge effects on the interaction and distribution of

26   three keystone species in South American temperate rainforests: the hemiparasitic

27   mistletoe *Tristerix corymbosus*, its main host (the liana *Campsidium valdivianum*) and

28   its only seed disperser (the marsupial *Dromiciops gliroides*).

29   3. The discordant impacts of forest edges on host (positive) and seed disperser (negative)

30   affected mistletoe distribution at large spatial scales, owing to the combined effects of

31   increased dispersal limitation and decreased host availability. More importantly,

32   marsupial abundance had contrasting effects on mistletoe abundance at small and

33   large spatial scales – suggesting a potential trade-off between local and long-distance

34   dispersal.

35   4. We found the number of adult mistletoes per host increased with host size, which

36   likely indicates that mistletoe colonization accumulated over the host's life-span.

37   However, the number of juveniles found per host peaked at medium-sized hosts,

38   increased with marsupial abundance and host availability and showed a negligible

39   response to edges.

40   5. Synthesis: The lack of spatial congruence between host and seed disperser probably

41   explains the scarcity of mistletoes in the study area, although the discordant drivers of

42   juvenile and adult distributions suggest that there is a trade-off between recruitment

43   patterns but also potential dispersal limitation at small scales. In essence, the

44   interdependence among species linked by (mutualistic and antagonistic) interactions

45   makes them more sensitive to anthropogenic disturbance, exacerbating its impact on

46   the diversity and functioning of forest ecosystems.

47 **Key-words**: *Campsidium valdivianum*, *Dromiciops gliroides*, edge effects, habitat

48 fragmentation, host-parasite interaction, seed dispersal, *Tristerix corymbosus*, trophic

49 interactions

50

Introduction

Species interactions are considered important elements of ecosystem functioning (Worm & Duffy 2003) and community stability (Thebault & Loreau 2005), which in turn represent two essential determinants of ecosystem resilience to disturbance (Gunderson 2000). For instance, species can be facilitated by interactions with other species when they provide nutrients, refuge, or reproduction, which leads to a match in the distribution of both interacting partners in order to fulfill their respectful requirements (Wisz *et al.* 2013). But the distribution and abundance of many species is also largely determined by their interactions with hosts, parasites and pathogens (Tack & Dicke 2013). These species interactions are especially relevant for sessile organisms (such as plants) whose reproduction and survival depends upon their relationships with many other guilds (e.g. pollinators, seed dispersers, mycorrhizae, herbivores, parasites or pathogens, and hosts).

Within the Anthropocene (sensu Crutzen 2002), the myriad threats faced by forests and other natural ecosystems across the world are having important impacts, not only upon the species that inhabit these natural habitats, but more importantly upon the functions they perform (Morris 2010; Herrera & Doblas-Miranda 2013) and on the interactions between them (Fagan, Cantrell & Cosner 1999; Tylianakis *et al.* 2008; Magrach *et al.* 2014). Species loss at the remaining forest fragments is often compounded by habitat degradation and edge effects, causing changes in the abundance and distribution of species (Murcia 1995) that in turn alter their interactions with other species (Magrach, Santamaría & Larrinaga 2013). While forest fragments have been classically approached as homogeneous units, both old-growth and managed forests may contain considerable environmental and biotic heterogeneity (Magrach, Larrinaga & Santamaría 2012). By facilitating human access to remaining forest fragments, fragmentation often entails further habitat heterogeneity disturbance – which tends to be larger at, but is not necessarily restricted to, the fragment's

4

76 edges (Magrach, Larrinaga & Santamaría 2012). Its effects include the creation of

77 anthropogenic gaps and tracks (e.g. by loggers, Magrach, Santamaria & Larrinaga 2012); the

78 disturbance or collection of animal species (e.g. by poachers Peres 2001); hydrological

79 disruption (Wu, Thurow & Whisenant 2000); and the reduction of understory cover (e.g., by

80 cattle and feral herbivores, Rodriguez-Cabal *et al.* 2013). Shifts in species distributions and

81 abundances at these forest boundaries lead to altered species interactions (Ewers, Bartlam &

82 Didham 2013), but the synergistic effect of environmental changes and alterations of species

83 interaction ensembles on species distributions has been largely unexplored and is thus still

84 difficult to predict (Herrera & Doblas-Miranda 2013).

85   In the particular case of plants, species are likely to be affected by disturbance

86 episodes, but those relying on mutualistic partners or exploiting antagonistic ones can be

87 expected to be particularly sensitive to them. Recent studies suggest that edge effects

88 (Magrach *et al.* 2014) have strong negative effects on seed dispersal, particularly for large-

89 seeded plants, while fragmentation can lead to species-specific changes in the amount of

90 herbivory suffered by different plants (Ruiz-Guerra *et al.* 2010), the combination of which

91 lead to important changes in the composition of plant communities in disturbed habitats

92 (Rodriguez-Cabal *et al.* 2013). It is therefore of paramount importance in order to strengthen

93 our ability to understand the effects of anthropogenic disturbances on plant communities, that

94 we take an integrative focus that examines the dynamic interplay between the spatial

95 distribution, the habitat requirements, and the sensitivity to disturbances of all interaction

96 partners. Unfortunately, monitoring programs addressing the effects of forest management

97 and/or restoration often focus on indicator species, assumed to reflect the state of the whole

98 ecosystem (Kremen 1992). Understanding the behavior of species complexes inter-related by

99 mutualistic and antagonistic relationships may therefore be vital to identify proper indicators

100   and interpret their responses in monitoring programs assessing the status and trends of

101   biodiversity in natural and managed forests.

102   In this paper, we analyze the impact of edge effects on a three-species interaction

103   complex inhabiting the temperate rainforests of southern South America: the mistletoe

104   *Tristerix corymbosus*: its host, the liana *Campsidium valdivianum*, and its only seed disperser,

105   the arboreal marsupial *Dromiciops gliroides* (Amico & Aizen 2000). Previous studies suggest

106   that the distance to the forest edge has a positive effect on flower visitation and fruit

107   production for this mistletoe species and hence that fruit availability increases at the interface

108   between the forest and the surrounding non-forest habitat (Magrach, Santamaría & Larrinaga

109   2013; Fontúrbel, Jordano & Medel 2015). Contrastingly, and although the marsupial *D.*

110   *glirodes* is predominantly frugivorous during the Austral summer, it is considered a forest

111   specialist species, (Marshall 1978; Hershkovitz 1999) which likely suggests that it avoids

112   forest edges. And indeed, fruit removal by this species decreased near forest edges (Magrach,

113   Santamaría & Larrinaga 2013). Taking into account the contrasting effects of forest edges on

114   pollination and seed dispersal and the exclusive dependence of the mistletoe species on its

115   host and seed disperser in the study area our main objective is to evaluate whether edge

116   effects (if any) on mistletoe distribution are caused by host availability, marsupial

117   distribution, habitat quality or a combination thereof. For this purpose, we evaluated at three

118   spatial scales: (i) the effects of habitat quality and distance to forest edges on the distribution

119   of mistletoes *T. corymbosus*, (ii) the extent to which host and marsupial distribution

120   contribute to such edge and/or habitat effects, and (iii) the relationship between mistletoe

121   recruitment (fruit production and juvenile abundance) and distribution (adult abundance). We

122   performed the analyses at three spatial scales: between host patches (>20m), within host

123   patches (<5m) and within host (i.e. per host individual); and using three different indicators

124   of habitat quality (tree density, canopy cover and bamboo cover). The results of our work

125   may be used to elicit the potential of two of these organisms, the mistletoe *Tristerix*

126   *corymbosus* and the marsupial *Dromiciops gliroides*, as indicators of ecosystem health in

127   Chile's (fragmented) austral rainforests.

128

129   **Material and Methods**

130   *Study species*

131   *Tristerix corymbosus* (L.) Kuijt (Loranthaceae) is a hemiparasitic mistletoe inhabiting the

132   temperate rainforests of southern Argentina and Chile. Although it parasites more than 25

133   plant species across its distribution range (Amico 2007), at the forests of Chiloé Island

134   (Southern Chile; see Study site; Fig. 1) it is hosted almost exclusively by the vine

135   *Campsidium valdivianum* (Phil.) Skottsb. and occasionally by *Rhaphithamnus spinosus*

136   (Juss.) Moldenke. It produces red tubular flowers grouped in inflorescences of 4–14 flowers,

137   pollinated mainly by the hummingbird *Sephanoides sephaniodes* Lesson (Aizen 2003). Fruits

138   are single-seeded green berries. Seeds are only able to germinate following passage through

139   the gut of its only disperser, the marsupial *Dromiciops gliroides* Thomas (Amico & Aizen

140   2000; Amico, Rodriguez-Cabal & Aizen 2011).

141   *Campsidium valdivianum* (Phil.) Skottsb. (Bignoniaceae) is a woody vine or liana,

142   growing up to 15 m in height, found in the temperate rainforests of southern Argentina and

143   Chile. It produces hermaphroditic tubular flowers, pollinated mainly by the hummingbird

144   *Sephanoides sephaniodes* (Smith-Ramirez 1993; Smith-Ramirez & Armesto 1994; Aizen &

145   Ezcurra 1998). Its fruits are dry ellipsoid capsules bearing winged, wind-dispersed seeds

146   (Marticorena *et al.* 2010).

147   *Dromiciops gliroides* is a small-sized arboreal marsupial restricted to the temperate

148   forests of southern South America (Saavedra & Simonetti 2001), where it plays an important

149   ecological role as the disperser of up to 80% of fleshy-fruited plants (Aizen 2005; Amico,

150   Rodriguez-Cabal & Aizen 2009) and the sole disperser of *T. corymbosus* (Amico & Aizen

151   2000). It is reported to depend strongly upon the presence of old-growth beech-dominated

152   forests (*Nothofagus* sp.) with bamboo (*Chusquea* sp.) in the understory (Marshall 1978;

153   Hershkovitz 1999). However, it is also found in Valdivian forests dominated by Myrtaceae

154   species (Martin 2010). Given the accelerated rates of loss and fragmentation faced by both

155   types of forests in Argentina and Chile (Echeverria *et al.* 2008), the species has been

156   classified as near threatened (Diaz & Teta 2008).

157   *Study site*

158   Our study was conducted within a 433 ha fragment of native, old-growth forest in Chiloé

159   Island (Southern Chile; Fig. 1). The island supports a variegated mosaic of old and secondary

160   growth forests, shrublands and prairies. Woodlands are a mixture of Valdivian and North-

161   Patagonian temperate rainforests, dominated by broad-leaved evergreen species (e.g.

162   *Tepualia stipularis* and *Amomyrtus luma*, Fam. Mirtaceae) covered by a rich diversity of vine

163   and epiphytic species, with numerous logs and snags, a dense undergrowth of bamboo

164   thickets (*Chusquea* sp.), and shrub-covered gaps and open areas (Armesto & Figueroa 1987).

165   Climate is temperate-humid subjected to a strong oceanic influence (annual precipitation:

166   2124 mm, mean temperature: 8.7 °C ,Salinas 2008).

167   We developed a Geographical Information System (GIS) for the study area, based on

168   1:5000-scale ortophotographs that included a layer of digitized forest cover (Fig. 1), over

169   which we overlaid a grid of 424 20 x 20 square cells (encompassing ~ 17 ha of the 433 ha for

170   the whole forest). Each cell's distance to the nearest forest edge was calculated from the

171   cell's centroid.

172   *Plant sampling*

173   During January 2008 we sampled each cell and recorded the presence and abundance of the

174   mistletoe *T. corymbosus* and that of its main host *C. valdivianum*. Within a 5 m radius of the

175   sampling point (located at the centroid of each 20 x 20 m cell), we recorded the presence and

176   abundance of *T. corymbosus* and *C. valdivianum* (from the ground and using binoculars), as

177   well as a suite of habitat characteristics that could influence the distribution of mistletoe, host

178   and seed disperser; namely, (i) the number of trees (the main hosts for the liana *C.*

179   *valdivianum)*, (ii) the proportion of canopy cover (visual estimation), and (iii) the proportion

180   of bamboo (*Chusquea quila*) cover in the understory as it affects habitat preference by the

181   marsupial *D. gliroides* (Rodriguez-Cabal & Branch 2011).

182   During January and February 2009, we re-surveyed the subset of cells where the host

183   was present in the 2008 survey (see Fig. 1). Using the same 5-m radius, we recorded the

184   number of mistletoes and hosts belonging to each of the following size classes. For the host

185   (*C. valdivianum*), size classes were based on the stem diameter at 1.3 m above the rooting

186   point, using four visual categories: small (<5 mm), medium (<10 mm), large (<15 mm) and

187   extra-large (>15 mm). To ensure consistency, visual assignations were always performed by

188   the same observer (JRP) and their accuracy was tested by comparing the visual categorization

189   to actual measurements of the stem diameter (to the nearest mm, using a digital calliper) for a

190   sub-sample of 1513 plants. Lack of significant differences between measured and visual

191   categories (two-way chi-square test: $\chi 2$=12.0; d.f.=9; p=0.213) confirmed that our method

192   worked well (i.e. 92.3, 82.9, 75.2, and 85.7% of small, medium, large and extra-large plants

193   were classified correctly). For *T. corymbosus* individuals we recorded length, width, height

194   and number of fruits; all measures were visually assigned by JRP given that many plants

195   were located above 2 m in height (c. 78% of adults; unpublished data). In order to be more

196   conservative with our visual estimations, we further assigned each mistletoe individual to a

197   size/age class of juveniles (<0.10 m^3) and adults (>0.10 m^3) after calculating their ellipsoid

198   volume. The presence/abundance of fruits could be also a measure to classify age class but

199   we found that the majority of size/age class of adults bear no fruit (c. 13% of adults;

200   unpublished data).

201   *Animal tracking*

202   We radio-tracked 16 *D. gliroides* individuals using PIP3 Ag392 tags, Biotrack®, which were

203   held using a harness made of surgical tape. Tag plus harness never weighed more than 5% of

204   the individual's weight. Previous tests using two individuals in captivity indicated that the

205   harness lasted at least a week, after which the tape lost adherence and the harness fell. We

206   carried out the sampling in two different periods; the first one in March 2008 where we

207   tracked seven individuals for seven consecutive nights and the second one during March

208   2009, when we tracked nine individuals during eight consecutive nights. Individuals tracked

209   in 2008 were marked using ear tags to ensure that they were different from those tracked in

210   2009. They included males, females and juveniles (see Table S1 for gender, weight and age

211   data on each individual). All individuals were trapped within the same forest fragment where

212   all observations and distribution models described in this study were carried out, using traps

213   baited with banana and placed above-ground and over the branches of trees (Fontúrbel &

214   Jiménez 2009). We calculated individual locations using triangulation from bearings taken

215   with three or four (2009 and 2008 respectively) receivers (Televilt® RX900 and Telonics®

216   TR4) located in previously geo-referenced points (GPS diferencial Topcon® GMS2, updated

217   to get GLONASS satellites). Before each tracking period we determined the triangulation

218   error using 15 tags distributed all over the study area, which we tracked by placing our three

219   (or four) receivers across all the possible combinations that arise from the use of six initial

220   reception points. These data were used both to select the best spatial configuration of our

221   reception points and to estimate the relocation error. We finally associated the position of

222   each individual seed disperser with the identity of the 424 20 x 20 cells within the study site

223   (Fig. 1).

224   To obtain a spatially-explicit estimate of the probability of visitation (thus of fruit

225   consumption) by marsupials at each grid cell within the study area, we proceeded in three

226   steps. First, we estimated the home-range utilized by each radio-tracked individual based on

227   its Utilization Distribution (UD). The UD is the probability density function that describes the

228   chances of finding that individual animal at a given point, based on the spatial distribution of

229   all its relocations (Worton 1995; Calenge 2006). We assumed that UD follows a bivariate

230   normal distribution, estimated the smoothing or 'window size' parameter (h) by means of the

231   "ad-hoc method" (Worton 1995), and defined the limit of the UD area enclosing the 95th

232   percentile of the bivariate function. In order to reduce potential biases in kernel density

233   estimation, we used only those individuals for which a minimum of 30 relocations were

234   recorded (10 out of 16) (Girard *et al.* 2002).

235   Second, we modeled the habitat preferences of each individual marsupial, taking into

236   account solely the habitat availability within such individual's home-range. For each cell

237   included in the individual´s home-range area, we modeled the effect of four habitat

238   characteristics (distance to edge, canopy cover, number of trees and bamboo cover) on

239   marsupial visitation probability (estimated as the number of relocations per cell, including a

240   value of zero for cells with no relocation but included within the home-range (see Figure S3

241   and for an equivalent procedure see also Rodríguez-Pérez, Wiegand & Santamaria 2012).

242   Third, based on the habitat characteristics of each surveyed cell, we used the model

243   estimates to infer the probability of visitation by the overall population of marsupials (relative

244   to that in all other cells), which can be considered as a proxy for marsupial abundance across

245   the fragment (Boyce *et al.* 2015). Such an assumption is based on the relationship between

246   the frequency of relocation of an individual and its abundance, which has been seen to hold

247 true when the species is at its carrying capacity (Rodríguez-Pérez, Wiegand & Santamaria

248 2012; Boyce *et al.* 2015). The lack of differences found between population sizes in disturbed

249 and old-growth forests (Celis-Diez *et al.* 2012) in our study area suggest this is the case for

250 our focal marsupial species. (It is worth noting, however, that our subsequent analyses are

251 based on visitation probabilities, i.e. an explicit relationship with abundance was not

252 required.) Finally, we used the output of the previous model to predict the probability of

253 relocating a marsupial per cell ("fitted marsupial abundance" hereafter), which was entered as

254 an independent variable in ensuing models targeting mistletoe presence and abundance (see

255 below).

256 *Data analysis*

257 First, we compared the spatial autocorrelation of the three variables we use as indicators of

258 habitat quality (the number of trees, canopy and bamboo cover) and the presence and

259 abundance of the three focal species (the mistletoe, its host and its main seed disperser, the

260 marsupial). We used Mantel correlograms at different distance-lags, followed by pair-wise

261 comparisons (spatial agreement between pairs of variables) using partial Mantel tests.

262   Second, we evaluated the relationship between the three indicators of habitat quality

263 and the distance to the nearest forest edge using Generalized Linear Models (GLMs

264 hereafter) with Poisson error distributions and log link functions.

265   Third, we modeled the effect of the three indicator variables of habitat quality on the

266 presence and abundance of the three focal species using GLMs, and Generalized Linear

267 Mixed effect Models (GLMMs hereafter). We generated all possible subsets of the full model

268 and following and information-theoretic approach selected the most parsimonious one based

269 on their AICc score (models with ΔAICc < 2 were considered equally plausible,Burnham &

270 Anderson 2002). Residuals from best performing models were checked for spatial

271 autocorrelation by means of Mantel correlograms. All independent variables were

272   standardized to allow for direct comparisons between effect sizes. Collinearity between pairs

273   of independent variables was tested using variance inflation factors (*vif*). All variables were

274   kept in models, since none of them showed *vif* > 3. Below we described the analysis details

275   for each focal species:

276   Host abundance: The full model included: distance to the nearest forest edge and the

277   three indicators of habitat quality (tree density, canopy and bamboo cover). Given potential

278   non-linear effects of distance to the forest edge in this case we also included a quadratic term

279   for this variable. GLMs were fitted using Poisson error distributions and log link functions.

280   Marsupial abundance: The full model included distance to the nearest forest edge, a

281   quadratic term for this variable, and the three indicators of habitat quality (as above), plus one

282   random factor (marsupial individual, n=10) and one offset (log of number of locations

283   divided by number of cells within the individual's home range; a constant additive term in the

284   linear predictor included in the model to control for its potential effects on the dependent

285   variable). GLMMs were fitted using zero-inflated Poisson error distributions and log link

286   functions. Parameter values from the best model were used to estimate predicted abundances

287   per cell ("fitted marsupial abundance" hereafter), which were entered as an independent

288   variable in ensuing models (see below).

289   Mistletoe presence and abundance: In order to evaluate whether the effects of habitat

290   quality and distance to the nearest forest edge were driven by the abundance of the host

291   and/or seed disperser, we fitted two types of GLMs to each of four dependent variables

292   describing mistletoe presence and abundance at three spatial scales: between host patches

293   (>20m: presence and abundance per sampling cell), within host patches (<5m: abundance per

294   host and proportion of hosts infected, within each sampling cell) and within host (abundance

295   per host individual, with cell as a random factor). Presence per cell was measured across the

296   entire sampled grid during the 2008 field survey, while the other three variables were

297   measured only in cells in which the host was present during the 2009 survey. The first type of

298   GLMs (hereafter model 1) included a full model with distance to the nearest forest edge, a

299   quadratic term for this variable given potential non-linear effects, and the three indicators of

300   habitat quality (as above), and all possible subsets thereof. The second type of GLMs

301   (hereafter model 2) included a full model with all previous variables, plus the abundance of

302   host and the abundance of marsupials, and all subsets thereof. Whenever significant edge or

303   habitat-quality effects found in model 1 were replaced by significant effects of host and/or

304   seed disperser in model 2, we conclude that such edge and/or habitat quality effects were

305   mediated by the partner species (i.e. by the availability of hosts and/or seed dispersers). Error

306   distribution and link function were respectively: binomial error with logit link for presence

307   per cell and presence per host, zero-inflated negative binomial error with log link for

308   abundance per cell, and zero-inflated Poisson error with log link function for abundance per

309   host.

310   Mistletoe recruitment: We evaluated juvenile abundance as a *proxy* for mistletoe

311   recruitment, and fruit production of adult mistletoes (which, in our study system, was highly

312   correlated with fruit removal, Magrach, Santamaría & Larrinaga 2013) to two types of full

313   models (and all possible subsets thereof), respectively including:

314   -   Model 1: distance to the nearest forest edge, a quadratic term of this variable, the

315   three indicators of habitat quality (as above) and the number of adult mistletoes.

316   -   Model 2: model 1's six variables, plus the abundance of hosts and (for juvenile

317   abundance) the marsupial abundance. To account for the effect of host size,

318   however, we used three separate variables each describing the abundance (number

319   of individuals per sampling cell) of hosts within different size classes (medium,

320   large and extra-large; small-sized hosts were not included because they never

321   hosted any mistletoes).

322   For both variables and both types of models, we used zero-inflated Poisson error

323   distributions and log link functions. All analyses were performed within the R environment

324   (R Development Core Team 2005).

325

326   **Results**

327   **<u>Presence, abundance and distribution:</u>** We found the host plant, *C. valdivianum,* in 46.4%

328   of the surveyed cells (197 out of 424), where it ranged in abundance from one to 29

329   individuals (6.60 ± 5.43, always referring to mean ± SD hereafter). The marsupial *D.*

330   *gliroides* was relocated in 37.5% of the surveyed cells (159 out of 424), where it was found

331   from one to 44 times (1.25 ± 4.13). The mistletoe, *T. corymbosus* was present in 43.4% of the

332   cells where its host was present (85 out of 197, equivalent to 20% of 424 cells), ranging from

333   one to 15 (2.96 ± 2.34) individuals per cell and zero to 13 (0.25 ± 0.98) individuals per host.

334   Hosts, marsupials and mistletoes were found at, respectively, nine to 190 metres (88.99 ±

335   45.20), 14 to 200 metres (104 ± 47.47) and nine to 160 metres (78.23 ± 43.12) from the

336   nearest forest edge, i.e. over the full range of surveyed distances (from 0 to 208 m). The

337   survey covered a very broad range of values of canopy cover (53.90 ± 20.93, range 5–95 %),

338   bamboo cover (8.76 ± 17.96, range 0–80%) and tree density (35.69 ± 28.81, range 0–335).

339   Habitat quality differed between forest interiors and edges, with more bamboo, less trees and

340   less canopy cover towards the interior of the forest (Fig. S2).

341   Spatial aggregation patterns differed for the abundance of the animal and both plant

342   partners. Host and mistletoe were significantly aggregated at small and medium distances (up

343   to 240 m, Fig. S1), but the marsupial was aggregated at small (<80 m) and large (>320 m)

344   distances and segregated at intermediate distances (120–280 m).

345   **<u>Host abundance.</u>** Host abundance was higher in denser tree stands with more canopy

346   cover and less bamboo cover, and showed also a slight, positive response to the proximity to

15

347 forest edges (Fig. 2, Table 1a). The only alternative, equally-parsimonious models differed

348 solely in the absence of an effect of canopy cover (Table S2a).

349 **Marsupial abundance:** Home range sizes of marsupial individuals ranged from 1.17

350 to 5.24 ha (3.11 ± 1.05). Several individuals dwelt exclusively in the forest interior, but others

351 visited also the forest edges (Fig. S3). Overall, they preferred areas with low bamboo cover

352 and tree densities and showed a negative response to forest-edge proximity (Fig. 2, Table 1b).

353 The three alternative, equally parsimonious models showed significant edge effects, but

354 differed in the inclusion of a non-significant quadratic edge effect (in one) as well as the

355 indicators of habitat quality included (tree density and bamboo cover in all three, canopy

356 cover in one; Table S2b).

357 **Mistletoe presence and abundance.** At a large scale (across all grid cells), mistletoe

358 presence increased towards forest edges and in areas with less bamboo cover (model 1; Fig.2,

359 Table 1c). The four alternative models differed only in the inclusion of one additional

360 variable: either tree density or canopy cover and the substitution of the quadratic edge effect

361 by a linear one (Table S2c). These effects were caused to some extent by the influence of

362 both partner species: when the model included these factors, there was a strong, positive

363 effect of host abundance and a weak, positive effect of marsupial abundance (model 2; Table

364 1d, Fig. 3). However, the abundance/activity of both interaction partners may not account

365 fully for edge effects as this variable still shows an important effect on mistletoe presence,

366 which increases near forest edges. In addition, the five alternative models included also an

367 edge effect (linear or quadratic) or a habitat quality (either canopy cover or bamboo cover)

368 effect.

369 At a medium scale (i.e. within the grid cells where the host was present), mistletoe

370 was more abundant in patches with high tree density and low bamboo cover (Table 1e), with

371 alternative models including an edge effect (linear or quadratic) as well as the effect of

canopy cover (one model, Table S2e). The tree density effect was mainly driven by the

positive effect that this variable has over the host as its effect disappeared when including

host abundance in model 2 (Table 1f). Alternative models included linear or quadratic edge

effects, marsupial abundance and/or other habitat quality indicators (canopy cover or tree

density, Table S2f).

At a small scale (i.e. per host individual) we found mistletoe abundance increased

with host size (Table 1g). Alternative models differed in the inclusion of an additional

variable, bamboo or canopy cover. These effects were modified by the inclusion of marsupial

abundance (Table 1h), which had a significant negative effect on mistletoe abundance per

host, overriding that of host width with alternative models including only the marsupial's

negative effect or an additional canopy cover one. In contrast, the proportion of hosts

colonized by mistletoes was not affected by any of the indicators of habitat quality: the best

model only included a non-significant effect of bamboo cover (for both models 1 and 2;

Table 1i,j). The only alternative model included also a single, though different indicator of

habitat quality: canopy cover (Table S2i,j).

Mistletoe recruitment: We found juveniles in 75% of the cells containing adult

individuals and across host sizes medium-sized hosts were the most abundant being

represented in 91% of the surveyed cells, followed by small hosts found in 89% of surveyed

cells. Mistletoe juveniles were more abundant in sites with more bamboo and adult

mistletoes (Table 1k). Alternative models included other habitat variables (canopy cover in

three and bamboo cover in five models) as well as a linear forest edge effect (Table S2k).

These effects were partly mediated by the interaction with partner species: models including

host and marsupial abundance showed significant, positive effects of (medium-sized) host

density and marsupial abundance, as well as positive effects of bamboo cover and adult

mistletoe abundance, a significant albeit negligible negative quadratic edge effect and a non-

17

397   significant effect of large host abundance (Table 1l, Fig.3). All alternative models kept the

398   significant, positive effects of adult mistletoe abundance, medium-sized host abundance,

399   marsupial abundance and bamboo cover; while some of them included the effect of tree

400   density (one model) or extra-large host plants (two models) (Table S2l). Mistletoe fruit

401   production increased towards forest edges and in areas with less bamboo and canopy cover,

402   and lower tree densities (as well as in grid cells with more adult mistletoes; Table 1m) with

403   no alternative models (Table S2m). The resulting model was not modified by the inclusion of

404   host abundance (Table 1n, S2n).

405   Residuals from the best models explaining the different variables measured were not

406   spatially autocorrelated (Mantel tests: $P>0.05$ in all cases), except in the case of mistletoe

407   juveniles – in which we found significant spatial autocorrelation at very small and very large

408   distances (Fig. S4). This means that our models explained successfully the spatial

409   autocorrelation found in the predicted variables.

410

411   **Discussion**

412   Our results indicate that the presence and abundance of the mistletoe *Tristerix corymbosus*

413   depends largely on host availability and habitat quality, but also on the activity of its main

414   seed disperser, the marsupial *Dromiciops gliroides.* Such dependence probably represents a

415   limiting factor for mistletoes, exacerbated by the fact that the host and the marsupial had

416   contrasting distributions: the former was more abundant near forest edges and decreased

417   towards the forest interior, while the latter was more likely found within forest interiors. This

418   result contrasts with previous studies suggesting that resource tracking by this marsupial

419   frugivore results in a spatial matching between mistletoe adults and recruits, facilitating

420   mistletoe dispersal to new hosts (García, Rodríguez-Cabal & Amico 2009). The spatial

421   coupling between hosts and marsupials found in previous studies (García, Rodríguez-Cabal &

422   Amico 2009) reinforces the regeneration of mistletoe populations while a spatial mismatch

423   between mistletoe resources that we find here (likely generated by habitat disturbance) can

424   lead to complex spatial patterns during mistletoe recruitment.

425   In our study area mistletoe distribution was likely affected by the distance to forest

426   edges at both large and small spatial scales. Such edge effects, however, were primarily

427   explained by host availability, which peaked nearby forest edges. These distributional

428   patterns, fully explained by our models (since they accounted for the spatial autocorrelation

429   found in the dependent variables), reflect the signature of mistletoe recruitment patterns but

430   are not fully accounted for by them. On the one hand, mistletoe fruit production increased

431   nearby edges and with low bamboo cover, potentially contributing to an increase in local seed

432   rain and marsupial visitation and activity in forest edges. Marsupials visited forest edges and

433   interiors, albeit with different probabilities, which probably reflects individual differences in

434   habitat preference in response to habitat heterogeneity (Piazzon et al unpublished data).

435   Despite our efforts during the field work (16 individuals were tracked), the number of

436   individuals used to estimate habitat preferences was fairly small (n=10). Although a larger

437   sample size would have been desirable to obtain more robust estimates of habitat preferences,

438   previous studies targeting the same species used similar sample sizes (n=14 in Fontúrbel *et*

439   *al.* 2010). More importantly, a previous study used an equivalent sample size of radio-tracked

440   frugivores (n=10 with the lizard Podarcis lilfordii, Rodríguez-Pérez, Wiegand & Santamaria

441   2012) to obtain reliable (habitat-based) estimates of frugivore visitation probability and

442   frugivore-mediated seed rain, which were validated using the distribution of adult and

443   juvenile plants. On the other hand, the abundance of mistletoe juveniles had a more complex

444   pattern: it increased with host availability and bamboo cover, as opposed to adult abundance,

445   which showed a negligible effect of the distance to the forest edge, and increased with

446   marsupial abundance (Rodriguez-Cabal, Aizen & Novaro 2007).

447   While the lack of spatial congruence between hosts and marsupials might be one of

448   the reasons behind the scarcity of mistletoes across the study area (present only in 20% of

449   cells surveyed), it is not necessarily the main driver behind the effects of forest edges on

450   mistletoe distribution- given that juvenile and adult distributions are not concordant. Instead,

451   positive effects of forest edges on host establishment/growth and mistletoe fruit production,

452   perhaps related to more suitable environmental conditions (e.g. higher irradiance), could

453   contribute to explain these discordant patterns (Lopez de Buen, Ornelas & García-Franco

454   2002; Aukema 2004). The strong effect of host abundance on mistletoe presence, reflected in

455   the spatial matching between the abundance of both plant species (which aggregate at

456   comparable distance-lags; Fig. S1), is also modulated by host size. While the number of adult

457   mistletoes per host increased with host size, the number of juveniles found per host peaked at

458   medium-sized hosts. The first result indicates the natural increase in mistletoe colonization

459   accumulated over the life-span of the host; while the second suggests a trade-off between host

460   size and mistletoe recruitment, mediated by the competition with more abundant, larger adult

461   individuals accumulated on the largest hosts.

462   Incorporating the spatial scale to our sampling and analysis proved to be important,

463   because the effects of the two main factors modulating dispersal and colonization (host and

464   marsupial abundance) increased in importance at larger scales. At the largest spatial scale

465   (mistletoe presence per grid cell), both had significant, positive effects; at the intermediate

466   scale (mistletoe abundance within each grid cell), only host abundance had significant

467   positive effects; and, at the smallest scale (i.e. per host individual), they had contrasting

468   effects on mistletoe abundance (positive for host abundance, negative for marsupial

469   abundance) and none of them influenced host colonization. This pattern is consistent with the

470   spatial scale at which dispersal limitation takes place in our study system. Mistletoes can only

471   grow on susceptible hosts (restricted, in our study area, to a single plant species: *C.*

472   *valdivianum*), which makes them highly dependent on directed seed dispersal by frugivores

473   (restricted, in our study area, to the marsupial *D. gliroides*).

474   The specific characteristics of such disperser, whose rapid displacements probably

475   compensate for the relatively short gut-passage times of ingested seeds, suggest that dispersal

476   events may involve the displacement of seeds across mistletoe patches (tens to hundreds of

477   meters; Piazzon et al., unpublished data) at moderately high frequencies. Still, at smaller

478   scales, dispersal seems to be very active: mistletoes were evenly spread amongst

479   neighbouring hosts and approx. 43% of hosts were infected by at least one mistletoe (a

480   proportion determined by the availability of large-enough hosts, see above). In such context,

481   the negative effect of seed-disperser abundance on local (per host) mistletoe abundance

482   probably reflects the increased "retrieval" of seeds from local patches, which are dispersed to

483   more distant ones (or succumb to digestion). This effect could be exacerbated by the positive

484   correlation between adult and juvenile mistletoes, should it reflect (besides the direct effects

485   of an increased seed source) the result of an increased attraction of frugivores by larger fruit

486   crops – as suggested by a recent analysis with stable isotopes, showing that isolated

487   mistletoes (*T. corymbosus*) dispersed by the marsupial *D. gliroides* have lower fruit removal

488   and larger dispersal distances than those in denser neighbourhoods (Morales *et al.* 2012). In

489   contrast, at large spatial scales (especially at >100 m, when the positive autocorrelation in

490   host abundance decreases) the autocorrelation in marsupial abundance becomes negative and

491   the proportion of colonized sites increases with marsupial abundance. Hence, dispersal

492   limitation is probably the factor behind the low proportion of occupied patches (<20% of grid

493   cells) and the clumped distribution of mistletoes.

494   The three species surveyed showed also a negative response to bamboo cover. In the

495   case of the host, the liana *C. valdivianum*, it probably reflects the effect of competition

496   between bamboo and liana's seedlings/saplings (such as Caccia, Chaneton & Kitzberger

497   2009), since a dense bamboo understory probably limits the amount of light and space

498   available for liana establishment and growth. In the case of the marsupial, the negative effect

499   of bamboo cover is in stark contrast with previous results asserting a positive relationship

500   between both (Hershkovitz 1999) – probably reflecting the switch in habitat requirements

501   from summer (when our study was conducted) to winter and spring (when hibernation and

502   reproduction take place). Bamboo presence is a key resource for nest production during

503   hibernation and breeding (Rodriguez-Cabal & Branch 2011); but our survey took place in

504   March, when the austral summer is coming to an end and the marsupial's activity is

505   dominated by the search for food (mainly insects and fleshy fruits) to increase its reserves for

506   hibernation (Amico, Rodriguez-Cabal & Aizen 2009). Alternatively, it might indicate an

507   association between bamboo cover and increased human disturbance, owing to the

508   predominance of such understory in anthropogenic gaps and logged areas (Gutierrez *et al.*

509   2008).

510

Conclusions

512   We found that disturbances (edge effects) affecting mistletoe distribution result from

513   the accumulation of the incongruent sensitivities of its plant (host) and animal (seed-

514   disperser) partners. While the immediate vicinity of edges proved positive for both plant

515   species (host and mistletoe), the preferences of the seed disperser (whose space use peaked at

516   forest interiors) suggests that a certain degree of disturbance associated to gaps and edges

517   may be beneficial for mistletoes. The discordant distributions of host and marsupial affected

518   mistletoe distribution at large spatial scales, owing to the combined effects of increasing

519 dispersal limitation and decreasing host availability in forest interiors. More importantly,

520 marsupial activity proved to have contrasting effects on mistletoe abundance at small and

521 large spatial scales – suggesting a potential trade-off between local and long-distance

522 dispersal in fragmented forests. Further, and contrary to previously assumed, forest edges in

523 old-growth forests may be beneficial for some key native species as they increase spatial

524 heterogeneity. Mapping such heterogeneity and understanding the factors and processes

525 affecting species interactions may prove of key importance to predict and manage

526 biodiversity in temperate rainforests, which are becoming increasingly degraded and

527 fragmented owing to anthropogenic pressure.

538 **Data accessibility**

539 Data deposited in Dryad repository (https://datadryad.org/resource/doi:10.5061/dryad.sp698)

540 (Magrach et al. 2015).

541 **Appendix A. Supplementary material**

542 Supplementary data associated with this article can be found, in the online version.

543

544 **References**

545 Aizen , M.A. (2003) Influences of animal pollination and seed dispersal on winter flowering
546   in a temperate mistletoe. *Ecology,* **84,** 2613-2627.
547 Aizen, M.A. (2005) Breeding system of *Tristerix corymbosus* (Loranthaceae), a winter-
548   flowering mistletoe from the Southern Andes. *Australian Journal of Botany,* **53,** 357-
549   361.
550 Aizen, M.A. & Ezcurra, C. (1998) High incidence of plant-animal mutualisms in the woody
551   flora of the temperate forest of southern South America: biogeographical origin and
552   present ecological significance. *Ecologia Austral,* **8,** 217-236.
553 Amico, G. & Aizen, M.A. (2000) Mistletoe seed dispersal by a marsupial. *Nature,* **408,** 929-
554   930.
555 Amico, G.C. (2007) Variacion geografica en la coloracion de los frutos del muerdago
556   *Tristerix corymbosus* (Loranthaceae): efecto de la historia evolutiva, del ambiente, de
557   los dispersores de semillas y de los hospedadores. Universidad Nacional del
558   Comahue, Argentina.
559 Amico, G.C., Rodriguez-Cabal, M.A. & Aizen, M.A. (2009) The potential key seed-
560   dispersing role of the arboreal marsupial *Dromiciops gliroides*. *Acta Oecologica,* **35,**
561   8-13.
562 Amico, G.C., Rodriguez-Cabal, M.A. & Aizen, M.A. (2011) Geographic variation in fruit
563   colour is associated with contrasting seed disperser assemblages in a south-Andean
564   mistletoe. *Ecography,* **34,** 318-326.
565 Armesto, J.J. & Figueroa, J. (1987) Stand structure and dynamics in the temperate rain forests
566   of Chiloe archipelago, Chile. *Journal of Biogeography,* **14,** 367-376.
567 Aukema, J.E. (2004) Distribution and dispersal of desert mistletoe is scale-dependent,
568   hierarchically nested. *Ecography,* **27,** 137-144.
569 Boyce, M.S., Johnson, C.J., Merrill, E.H., Nielsen, S.E., Solberg, E.J. & van Moorter, B.
570   (2015) Can habitat selection predict abundance? *Journal of Animal Ecology*, n/a-n/a.
571 Burnham, K.P. & Anderson, D.L. (2002) *Model selection and multi-model inference: A*
572   *practical information-theoretic approach.* Springer, New York, USA.
573 Caccia, F.D., Chaneton, E.J. & Kitzberger, T. (2009) Direct and indirect effects of
574   understorey bamboo shape tree regeneration niches in a mixed temperate forest.
575   *Oecologia,* **161,** 771-780.
576 Calenge, C. (2006) The package "adehabitat" for the R software: A tool for the analysis of
577   space and habitat use by animals. *Ecological modelling,* **197,** 516-519.
578 Celis-Diez, J.L., Hetz, J., Marín-Vial, P.A., Fuster, G., Necochea, P., Vásquez, R.A., Jaksic,
579   F.M. & Armesto, J.J. (2012) Population abundance, natural history, and habitat use by
580   the arboreal marsupial Dromiciops gliroides in rural Chiloé Island, Chile. *Journal of*
581   *Mammalogy,* **93,** 134-148.
582 Crutzen, P.J. (2002) Geology of mankind. *Nature,* **415,** 23-23.
583 Diaz, M. & Teta, P. (2008) *Dromiciops gliroides*. *Red List of Threatened Species* (ed. IUCN).
584 Echeverria, C., Coomes, D.A., Hall, M. & Newton, A.C. (2008) Spatially explicit models to
585   analyze forest loss and fragmentation between 1976 and 2020 in southern Chile.
586   *Ecological modelling,* **212,** 439-449.
587 Ewers, R.M., Bartlam, S. & Didham, R.K. (2013) Altered species interactions at forest edges:
588   contrasting edge effects on bumble bees and their phoretic mite loads in temperate
589   forest remnants. *Insect Conservation and Diversity,* **6,** 598-606.
590 Fagan, W.E., Cantrell, R.S. & Cosner, C. (1999) How habitat edges change species
591   interactions. *American Naturalist,* **153,** 165-182.

Fontúrbel, F.E. & Jiménez, J.E. (2009) Underestimation of Abundances of the Monito Del Monte (Dromiciops gliroides) due to a Sampling Artifact. *Journal of Mammalogy,* **90,** 1357-1362.

Fontúrbel, F.E., Jordano, P. & Medel, R. (2015) Scale-dependent responses of pollination and seed dispersal mutualisms in a habitat transformation scenario. *Journal of Ecology***,** n/a-n/a.

Fontúrbel, F.E., Silva-Rodríguez, E.A., Cárdenas, N.H. & Jiménez, J.E. (2010) Spatial ecology of monito del monte (Dromiciops gliroides) in a fragmented landscape of southern Chile. *Mammalian Biology - Zeitschrift für Säugetierkunde,* **75,** 1-9.

García, D., Rodríguez-Cabal, M.A. & Amico, G.C. (2009) Seed dispersal by a frugivorous marsupial shapes the spatial scale of a mistletoe population. *Journal of Ecology,* **97,** 217-229.

Girard, I., Ouellet, J.P., Courtois, R., Dussault, C. & Breton, L. (2002) Effects of sampling effort based on GPS telemetry on home-range size estimations. *Journal of Wildlife Management,* **66,** 1290-1300.

Gunderson, L.H. (2000) Ecological resilience- In theory and application *Annual Review of Ecology, Evolution and Systematics,* **31,** 425-439.

Gutierrez, A.G., Aravena, J.C., Carrasco-Farias, N.V., Christie, D.A., Fuentes, M. & Armesto, J.J. (2008) Gap-phase dynamics and coexistence of a long-lived pioneer and shade-tolerant tree species in the canopy of an old-growth coastal temperate rain forest of Chiloe Island, Chile. *Journal of Biogeography,* **35,** 1674-1687.

Herrera, J.M. & Doblas-Miranda, E. (2013) Land-cover change effects on trophic interactions: Current knowledge and future challenges in research and conservation. *Basic and Applied Ecology,* **14,** 1-11.

Hershkovitz, P. (1999) *Dromiciops gliroides* Thomas, 1894,last of the Microbiotheria (Marsupialia), with a review of the family Microbiotheriidae. *Fieldiana Zoology,* **93,** 1-60.

Kremen, C. (1992) Assessing the Indicator Properties of Species Assemblages for Natural Areas Monitoring. *Ecological Applications,* **2,** 203-217.

Lopez de Buen, L., Ornelas, J.F. & García-Franco, J.G. (2002) Mistletoe infection of trees located at fragmented forest edges in the cloud forests of Central Veracruz, Mexico. *Forest Ecology and Management,* **164,** 293-302.

Magrach, A., Larrinaga, A.R. & Santamaría, L. (2012) Internal Habitat Quality Determines the Effects of Fragmentation on Austral Forest Climbing and Epiphytic Angiosperms. *PLoS ONE,* **7,** e48743.

Magrach, A., Laurance, W.F., Larrinaga, A.R. & Santamaria, L. (2014) Meta-Analysis of the Effects of Forest Fragmentation on Interspecific Interactions. *Conservation Biology,* **28,** 1342-1348.

Magrach, A., Santamaria, L. & Larrinaga, A.R. (2012) Differential effects of anthropogenic edges and gaps on the reproduction of a forest-dwelling plant: The role of plant reproductive effort and nectar robbing by bumblebees. *Austral Ecology,* **37,** 600-609.

Magrach, A., Santamaría, L. & Larrinaga, A.R. (2013) Forest edges show contrasting effects on an austral mistletoe due to differences in pollination and seed dispersal. *Journal of Ecology,* **101,** 713-721.

Marshall, L.G. (1978) *Dromiciops australis. Mammalian species,* **99,** 1-5.

Marticorena, A., Alarcon, D., Abello, L. & Atala, C. (2010) *Plantas trepadoras, epifitas y parasitas nativas de Chile*. Concepcion, Chile.

Martin, G.M. (2010) Geographic distribution and historical occurrence of *Dromiciops gliroides* Thomas (Metatheria: Microbiotheria). *Journal of Mammalogy,* **91,** 1025-1035.

642 Morales, J.M., Rivarola, M.D., Amico, G. & Carlo, T.A. (2012) Neighborhood effects on
643   seed dispersal by frugivores: testing theory with a mistletoe–marsupial system in
644   Patagonia. *Ecology,* **93,** 741-748.
645 Morris, R.J. (2010) Anthropogenic impacts on tropical forest biodiversity: a network
646   structure and ecosystem functioning perspective. *Philosophical Transactions of the*
647   *Royal Society B: Biological Sciences,* **365,** 3709-3718.
648 Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends*
649   *in Ecology and Evolution,* **10,** 58-62.
650 Peres, C.A. (2001) Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on
651   Amazonian Forest Vertebrates. *Conservation Biology,* **15,** 1490-1505.
652 R Development Core Team (2005) A language and environment for statistical computing. R
653   Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.
654 Rodriguez-Cabal, M.A., Aizen, M.A. & Novaro, A.J. (2007) Habitat fragmentation disrupts a
655   plant-disperser mutualism in the temperate forest of South America. *Biological*
656   *Conservation,* **139,** 195-202.
657 Rodriguez-Cabal, M.A., Barrios-Garcia, M.N., Amico, G.C., Aizen, M.A. & Sanders, N.J.
658   (2013) Node-by-node disassembly of a mutualistic interaction web driven by species
659   introductions. *Proceedings of the National Academy of Sciences,* **110,** 16503-16507.
660 Rodriguez-Cabal, M.A. & Branch, L.C. (2011) Influence of habitat factors on the distribution
661   and abundance of a marsupial seed disperser. *Journal of Mammalogy,* **92,** 1245-1252.
662 Rodríguez-Pérez, J., Wiegand, T. & Santamaria, L. (2012) Frugivore behaviour determines
663   plant distribution: a spatially-explicit analysis of a plant-disperser interaction.
664   *Ecography,* **35,** 113-123.
665 Ruiz-Guerra, B., Guevara, R., Mariano, N.A. & Dirzo, R. (2010) Insect herbivory declines
666   with forest fragmentation and covaries with plant regeneration mode: evidence from a
667   Mexican tropical rain forest. *Oikos,* **119,** 317-325.
668 Saavedra, B. & Simonetti, J.A. (2001) New records of *Dromiciops gliroides* (Microbiotheria:
669   Microbiotheriidae) and *Geoxus valdivianus* (Rodentia: Muridae) in central Chile: their
670   implications for biogeography and conservation. *Mammalia,* **65,** 96-100.
671 Salinas, M.F. (2008) Diferenciacion de nichos ecologicos de tres especies de Gesneriaceas
672   epifitas del bosque templado del sur de Chile. PhD, Universidad de Chile.
673 Smith-Ramirez, C. (1993) Los picaflores y su recurso floral en el bosque templado de la isla
674   de Chiloe, Chile. *Revista Chilena de Historia Natural,* **66,** 65-73.
675 Smith-Ramirez, C. & Armesto, J.J. (1994) Flowering and fruiting patterns in the temperate
676   rainforest of Chiloe, Chile--Ecologies and climatic constraints. *Journal of Ecology,*
677   **82,** 353-365.
678 Tack, A.J.M. & Dicke, M. (2013) Plant pathogens structure arthropod communities across
679   multiple spatial and temporal scales. *Functional Ecology,* **27,** 633-645.
680 Thebault, E. & Loreau, M. (2005) Trophic interactions and the relationship between species
681   diversity and ecosystem stability. *American Naturalist,* **166,** 5.
682 Tylianakis, J., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and
683   species interactions in terrestrial ecosystems. *Ecology Letters,* **11,** 1351-1363.
684 Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann,
685   C.F., Forchhammer, M.C., Grytnes, J.A., Guisan, A., Heikkinen, R.K., Hoye, T.T.,
686   Kuhn, I., Luoto, M., Maiorano, L., Nilsson, M.C., Normand, S., Ockinger, E.,
687   Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P. &
688   Svenning, J.C. (2013) The role of biotic interactions in shaping distributions and
689   realised assemblages of species: implications for species distribution modelling.
690   *Biological Review of the Cambridge Philosophical Society,* **88,** 15-30.

691   Worm, B. & Duffy, J.E. (2003) Biodiversity, productivity and stability in real food webs.
692   *Trends in Ecology and Evolution,* **18,** 628-632.
693   Worton, B. (1995) Using Monte Carlo simulation to evaluate kernel-based home range
694   estimators. *Journal of Wildlife Management,* **59,** 794-800.
695   Wu, X.B., Thurow, T.L. & Whisenant, S.G. (2000) Fragmentation and Changes in
696   Hydrologic Function of Tiger Bush Landscapes, South-West Niger. *Journal of*
697   *Ecology,* **88,** 790-800.
698

699

700

701

702 **Table 1.** Results of Generalized Linear Models analyzing the effect of habitat quality and
703 distance to nearest forest edge forest edge (model 1) and habitat quality, distance to the
704 nearest forest edge, host abundance and seed-disperser abundance (model 2) on host and seed
705 disperser distribution (only model 1) and on several descriptors of mistletoe distribution
706 (modles 1 and 2). Host: *Capsidium valdivianum*. Seed disperser: *Dromyciops glirioides*.
707 Mistletoe: *Tristerix corymbosus*
708
709
710
711
712
713
714
715
716
717
718
719
720
721
722
723
724
725

	Estimate	SE	z value	Pr(>|z|)
a) Host abundance (#individuals/grid cell)				
(Intercept)	1.82	0.03	60.92	< 0.001
Distance to edge	-0.12	0.03	-3.80	**< 0.001**
Number of trees	0.10	0.02	4.71	**< 0.001**
Canopy cover	0.05	0.03	1.45	0.15
Bamboo cover	-0.26	0.04	-6.26	**< 0.001**
b) Seed disperser abundance (#relocations/grid cell)				
(Intercept)	-0.11	0.21	-0.52	0.60
Number of trees	-0.70	0.12	-5.94	**< 0.001**
Canopy cover	0.10	0.06	1.71	0.09
Bamboo cover	-0.40	0.08	-5.16	**< 0.001**
Distance to edge	0.82	0.28	2.94	**0.003**
Distance to edge^2	-0.44	0.26	-1.70	0.09
c) Mistletoe distribution, large scale (presence/grid cell) - model 1				
(Intercept)	-1.02	0.15	-6.88	**< 0.001**
Distance to edge^2	-0.38	0.15	-2.53	**0.01**
Bamboo cover	-0.05	0.01	-4.02	**< 0.001**
d) Mistletoe distribution, large scale (presence/grid cell) - model 2				
(Intercept)	-2.10	0.22	-9.57	**< 0.001**
Distance to edge^2	-0.80	0.35	-2.30	**0.02**
C. valdivianum abundance	2.12	0.23	9.41	< 0.001
Fitted *D. gliroides* abundance	0.59	0.25	2.30	**0.02**
e) Mistletoe abundance, medium scale (#individuals/grid cell) - model 1				
(Intercept)	0.70	0.10	7.20	**< 0.001**
Bamboo cover	-0.67	0.16	-4.23	**< 0.001**
Number of trees	0.15	0.05	2.87	**0.004**
f) Mistletoe abundance, medium scale (#individuals/grid cell) - model 2				
(Intercept)	0.28	0.12	2.29	**0.02**
C. valdivianum abundance	0.49	0.06	8.59	**< 0.001**
Bamboo cover	-0.45	0.15	-3.08	**0.002**
g) Mistletoe abundance, small scale (#individuals/host) - model 1				
(Intercept)	-0.74	0.20	-3.64	**< 0.001**
Distance to edge	-0.27	0.14	-1.94	0.05
C. valdivianum width	0.63	0.07	9.35	**<0.001**
h) Mistletoe abundance, small scale (#individuals/host) - model 2				
(Intercept)	-0.41	0.42	-1.00	0.32
C. valdivianum width	0.37	0.20	1.87	0.06
Fitted *D. gliroides* abundance	-0.82	0.31	-2.69	**0.007**
i) Host colonization, small scale (proportion of hosts colonized)- model 1				
(Intercept)	-2.07	0.33	-6.21	< 0.0001
Bamboo cover	-0.25	0.42	-0.59	0.56
j) Host colonization, small scale (proportion of hosts colonized)- model 2				
(Intercept)	-2.07	0.33	-6.21	< 0.0001
Bamboo cover	-0.25	0.42	-0.59	0.56

k) Juvenile mistletoe abundance, small scale (#individuals/host) - model 1				
(Intercept)	0.98	0.12	7.94	**< 0.001**
Adult *T. corymbosus*	0.38	0.06	6.43	**< 0.001**
Number of trees	0.14	0.08	1.82	0.06
Bamboo cover	0.21	0.08	2.59	**0.009**
l) Juvenile mistletoe abundance, small scale (#individuals/host) - model 2				
(Intercept)	0.84	0.13	6.25	**<0.001**
Distance to edge^2	-0.39	0.17	-2.24	**0.02**
Fitted *D. gliroides* abundance	0.57	0.18	3.19	**0.001**
Medium *C. valdivianum*	0.20	0.06	3.12	**0.002**
Adult *T. corymbosus*	0.45	0.07	6.58	**<0.001**
Bamboo cover	0.36	0.10	3.68	**<0.001**
Large *C. valdivianum*	0.21	0.11	1.93	0.05
m) Mistletoe fruit production (#fruits/grid cell) – model 1				
(Intercept)	-5.97	1.04	-5.76	**<0.001**
Distance to edge	-17.13	1.94	-8.84	**<0.001**
Distance to edge^2	-8.39	1.48	-5.67	**< 0.001**
Bamboo cover	-1.04	0.24	-4.30	**<0.001**
Adult *T. corymbosus*	7.76	1.02	7.60	**<0.001**
Number of trees	-0.17	0.08	-2.02	**0.04**
Canopy	-1.15	0.08	-14.68	**<0.001**
n) Mistletoe fruit production (#fruits/grid cell) – model 1				
(Intercept)	-5.97	1.04	-5.76	**<0.001**
Distance to edge	-17.13	1.94	-8.84	**<0.001**
Distance to edge^2	-8.39	1.48	-5.67	**< 0.001**
Bamboo cover	-1.04	0.24	-4.30	**<0.001**
Adult *T. corymbosus*	7.76	1.02	7.60	**<0.001**
Number of trees	-0.17	0.08	-2.02	**0.04**
Canopy	-1.15	0.08	-14.68	**<0.001**

726

727

30

728 **Figure legends.**

729 **Figure 1.** Location and spatial design of the mistletoe survey in Chiloé Island, Southern

730 Chile. a) Geographic location. b) Survey grid within the old-growth forest fragment (grey

731 area). Grid-cell size was 20 x 20 m. and c) Sampling area within each grid cell with hosts

732 infected by mistletoe in black and those not infected in white.

733 **Figure 2.** Partial residual plots showing the effect of selected environmental variables

734 (distance to edge, bamboo cover and number of trees) on the abundance of *C. valdivianum*,

735 the probability of relocating *D. gliroides* and the presence of *T. corymbosus* per surveyed grid

736 cell. Selection of independent variables and fitted lines are based on the best GLMM model

737 (see Table 1 for estimated parameters and Table S2 for all alternative models).

738 **Figure 3.** Partial residual plots showing the effect of habitat quality, distance to the nearest

739 forest edge, host abundance, host size and/or seed disperser relocation probability on the

740 distribution of adult and juvenile mistletoes (*T. corymbosus*). For mistletoe juveniles, models

741 included an additional predictor: adult mistletoe abundance. Selection of independent

742 variables and fitted lines are based on the best GLMM model (see Table 1 for estimated

743 parameters, Table S2 for alternative models).

744

745

746

747

Figure 1.
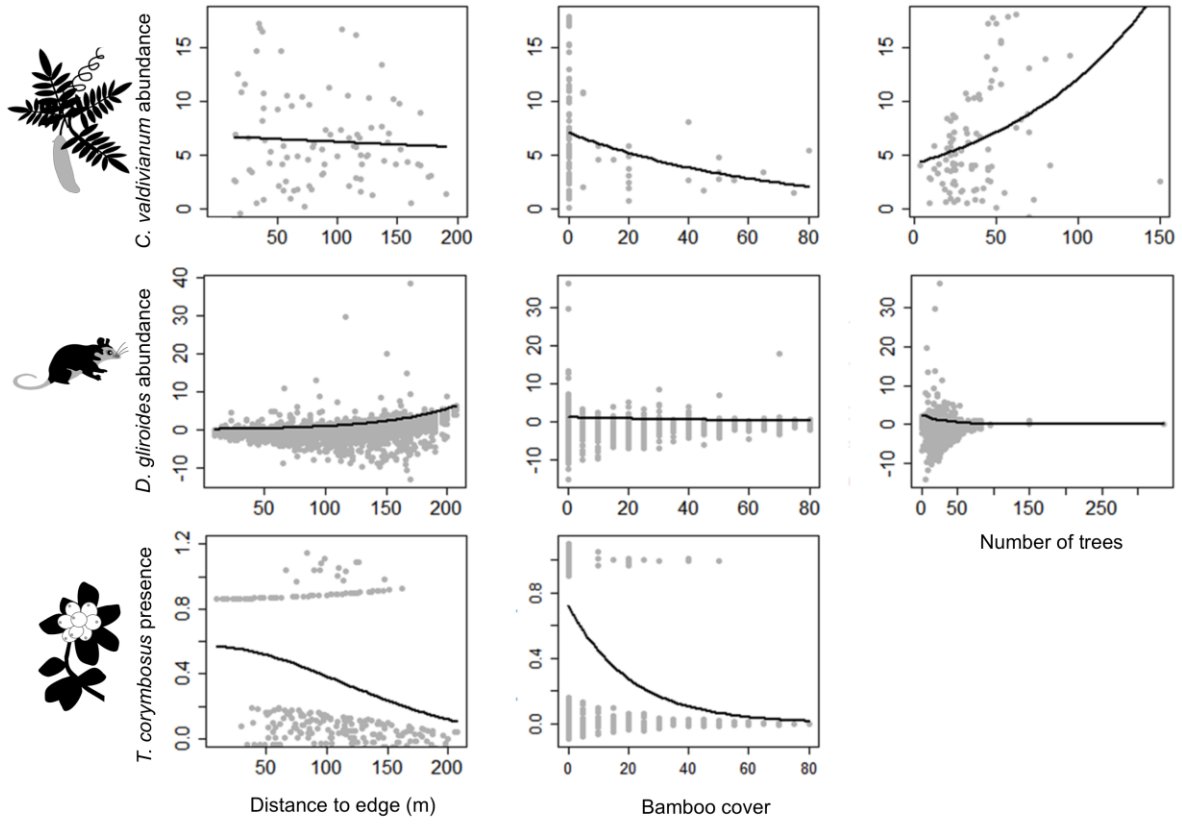
748
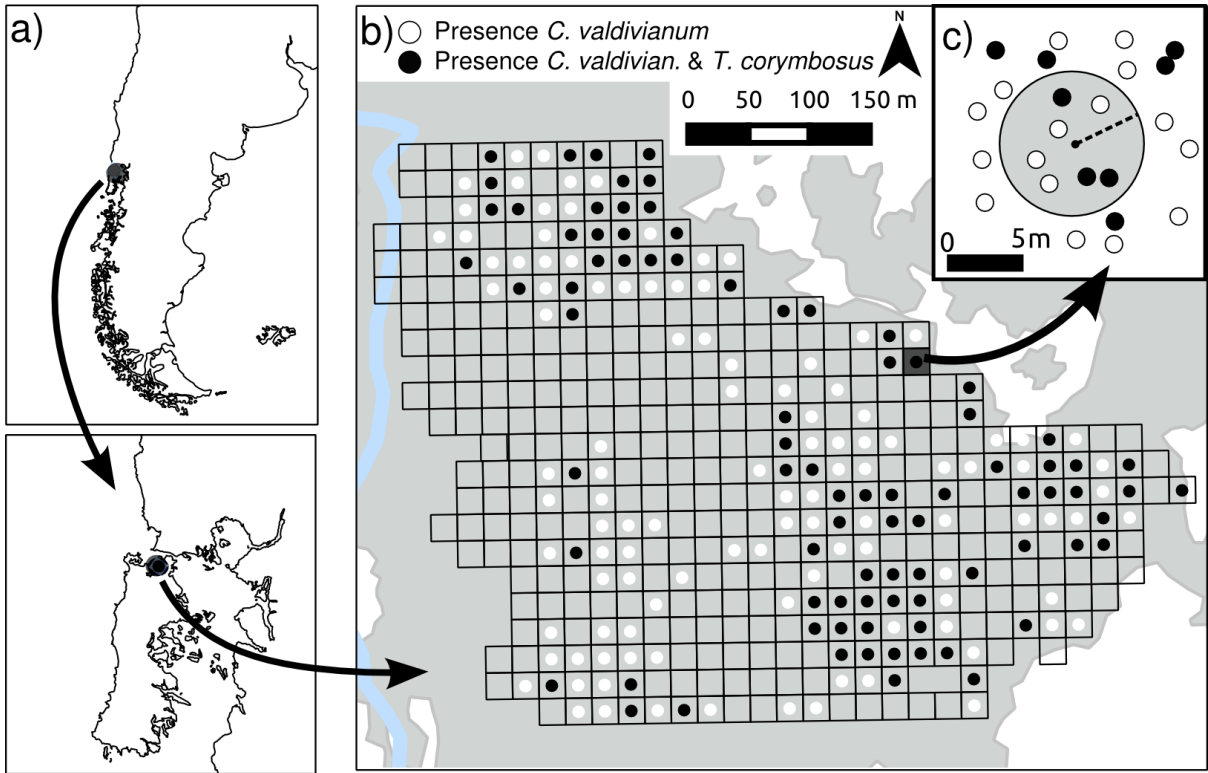
749

750

751

752

753
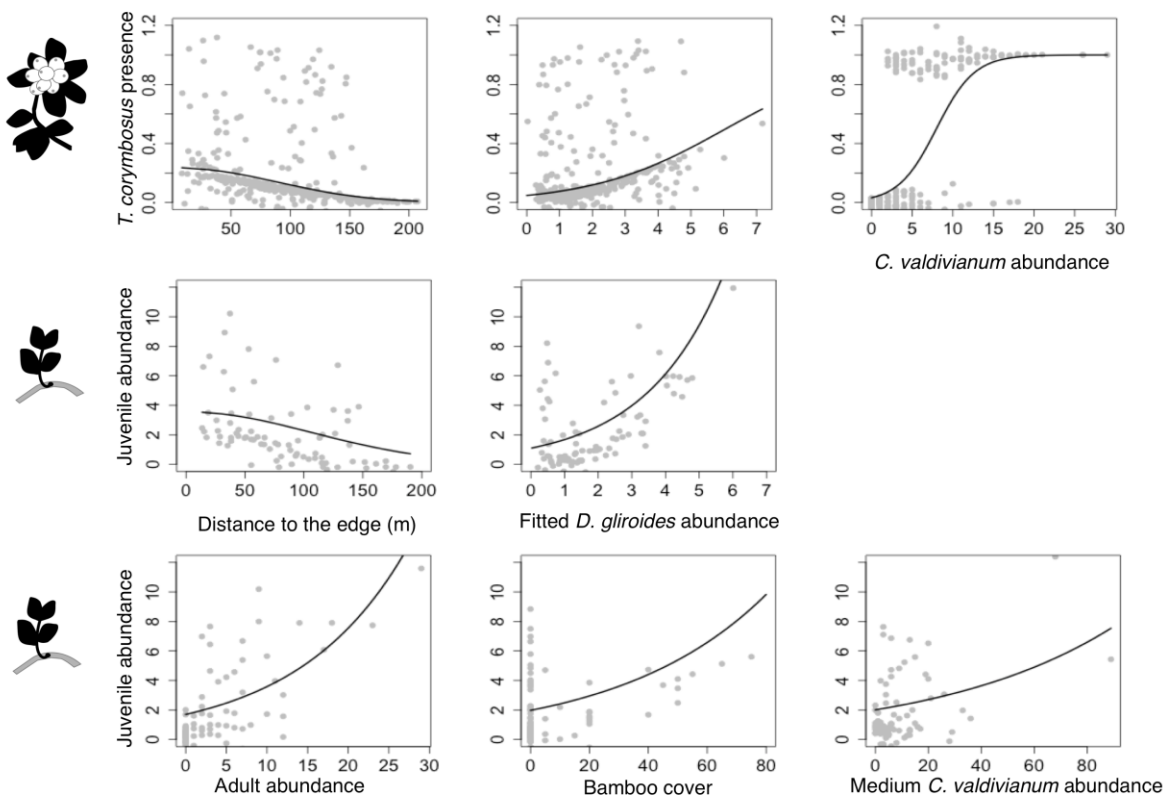
754

755

756

757

758

759

760

761

762

763

764 **Figure 2.**

765

766

Figure 3.

767

768

769

770

771
772

773

774

775

776

777

778