1 **The role of the geologic substrate on *Tillandsia recurvata* infestation and the**

2 **development of forest decaying on a semiarid oak forest**

3 "Forest decaying process regulated by geodiversity"

4

5 Ulises Rodriguez-Robles[1*], Tulio Arredondo[2*]

6 [1]Departamento de Ecología y Recursos Naturales. Centro Universitario de la Costa Sur.

7 Universidad de Guadalajara. Autlán de Navarro, Av. Independencia Nacional # 151,

8 Centro, 48900, Jalisco, México. URR (ulises.rodriguez@cucsur.udg.mx)

9 [2]División de Ciencias Ambientales, Instituto Potosino de Investigación Científica y

10 Tecnológica, Camino a la Presa de San José # 2055, Lomas 4ta, C.P. 78216, San Luís

11 Potosí, S.L.P., México. JTAM (tulio@ipicyt.edu.mx)

12

13 **Corresponding author:** Ulises Rodríguez Robles (ulises.rodriguez@cucsur.udg.mx) and

14 Tulio Arredondo Moreno (tulio@ipicyt.edu.mx)

15

Abstract

The Geodiversity involves substrate characteristics such as degree of fractured rock, fracture depth, soil depth, parental rock, soil texture, etc., that affect the hidrology of substrates and subsequently the availability of water for plants. Here we examined the importance of the geological substrate, as a factor that triggers the incidence of forest decline. We demonstrated that characteristics of the geological substrate related to the limitation of water availability enhances *Tillandsia recurvata* (*Tire*) infestation and eventually causes loss of vigor in oak trees. Using electrical resistivity tomography (geophysical methods) and stable isotope techniques ($\delta 18O$ / $\delta 16O$), we showed that substrates dominated by regolith and rocks imposed greater conditions of drought to an oak forest stand than a substrate with a more granulated material. Trees in this forest stand presented greater densities of *Tire*, a plant considered as epiphyte. However, under the observed conditions of high infestation, *Tire* apparently exhibited a change from epiphytic to parasitic plant as it acquired water from oak. This study identified that the structural composition of the substrate (i.e. geodiversity) is a factor accelerating the processes of decay and likely forest mortality related to the effects of drought and the infestation by pests and diseases.

Summary statement

Using geophysical methods we identified forests stands showing contrasting levels of infestation and decaying of trees that related to substrate composition such as; soil depth, rock fractures, reolithe material, etc. This was corroborated by identification of the sources of water by trees attesting that the less geodiverse substrates exhibited more damaged trees.

Type of article **- Original**

Number of words:

Abstract – **198**

Main text – **5862**

Number of references – **54**

Number of figures – **6**

Supporting Information – **3**

Introduction

As an emerging global phenomenon that is apparently related to factors triggering global environmental change, mortality of forest masses continuous increasing (Hartmann, Adams, Anderegg, Jansen, & Zeppel, 2015). Most recent reports of forest mortality are located in the South of Europa (Bigler, Bräker, Bugmann, Dobbertin, & Rigling, 2006; Bréda, Huc, Granier, & Dreyer, 2006), and the temperate and boreal forest in the west of North America and the Southeast of USA (van Mantgem et al., 2009), reaching ci. 10 million ha of damaged forest ever since 1997 (Raffa et al., 2008). This mortality of forest stands in several places of the planet has being associated to an increase of global temperatures and the incidence of droughts (Allen et al., 2010; N. McDowell et al., 2008), suggesting that forest ecosystems started to respond to global warming. If these trends continue and the forest mortality spreads even more, the consequences in several ecosystem services could become catastrophic, affecting processes such as direct carbon capture by the vegetation, enhancing C losses from vegetation sinks and altering feedback mechanisms between biosphere and atmosphere such as regional energy and water cycles (Allen et al., 2010).

So far, three hypotheses are proposed to explain the mechanisms operating with forest mortality including; hydraulic failure, carbon starvation, incidence of pests (N. McDowell et al., 2008). For this last aspect, although the presence of pests and pathogens (ex. miners, parasitic plants, fungus, etc.) in forest is a common aspect, it is hypothesized that its incidence and impact is exacerbated when conditions trigger either hydraulic failure or carbon starvation. In consequence trees reduce investment in the synthesis of chemical defenses (Netherer et al., 2015) against insects and diseases.

Although, the overall causes of forest mortality are already defined (Meddens et al., 2015) and there is a coincidence in pointing out that the trigger for these mechanisms are long term droughts. These are conditions that additionally favor a sharp increase in the vapor pressure deficit but also an abatement of water reservoirs in the superficial soil layers and even in the geologic substrate (i.e. rock fractures). Respect to the role of geological substrate, there are not many studies examining the role of the geologic composition at the landscape level as a factor for forest mortality, to find related patterns to the geologic

92   diversity. The geologic diversity (Geodiversity, sensu Gray, 2004) likely plays an important

93   role in the incidence of tree mortality. For instance, the degree of fractured rock, fracture

94   depth, soil depth, parental rock, soil texture, etc., are geologic characteristics of the

95   substrate that define conditions for plants to replenish their water during drought (Ulises

96   Rodríguez-Robles, Arredondo, Huber-Sannwald, Yépez, & Ramos-Leal, 2020). These

97   characteristics can either promote or delay forest decay or mortality. In a semiarid forest in

98   central México for instance, conditions provided by the geodiversity was the factor defining

99   whether two species, oak and pine, were found as pure or coexisting stands. Thus, a

100   substrate with the deepest soil (ci. 30 cm) but little fractured rock favored pure pine stands,

101   while shallow soils (ci. 20 cm) and a complex combination of fractured rock, rock pockets

102   and exfoliated rocks favored mixed forest stands (Ulises Rodríguez-Robles et al., 2020; U.

103   Rodríguez-Robles, Arredondo, Huber-Sannwald, Ramos-Leal, & Yépez, 2017). This

104   suggest that geodiversity might act as an additional factor in the patterns of drought at the

105   landscape level and therefore as a potential factor of decaying in forest stands.

106   Based on the theoretical framework related to the mechanisms causing forest mortality

107   (*sensu* McDowell 2008), if geodiversity increments conditions of climatic drought (ej.

108   lower rock fracturing, shallow soils, etc.) it is likely that we could also observe response

109   patterns in the forest, including a rise in insect pests and diseases, as suggests the third

110   mechanisms of mortality (Anderegg et al., 2015; Dietze & Matthes, 2014).

111   An initial monitoring in a semiarid oak forest in central Mexico, showed at the landscape

112   level distinctive infestation levels by *Tillansia recurvata (Tire)* that could relate to a 7 years

113   drought period (Fig. S1) as well as to the geologic features of the substrate. However,

114   observations as well as rural peasants' testimonies in this forest region suggest that

115   increases in *Tire* densities on trees come together with a decay in the tree condition and the

116   loss of tree foliage, with eventual tree mortality. *T. recurvata* performance and impact on

117   forest became an intense theme of debate regarding its role in shrublands and forests. *Tire*

118   is a specie reported as epiphyte, implying that uses trees just as a sitting place, with not

119   reported use of resources from the tree. However, in the last decade it has being associated

120   with the death of thousands of trees of various species, both coniferous and broadleaved,

121   and even vegetation typical of arid areas such as mesquite (Prosopis spp), huizache (Acasia

spp) and others (Aguilar-Rodríguez, Terrazas, Huidobro-Salas, & Aguirre-León, 2016; Cortes-Anzures, Corona-Lopez, Toledo-Hernandez, Valencia-Diaz, & Flores-Palacios, 2017; Lopez-Villalobos, Flores-Palacios, & Ortiz-Pulido, 2008). Some researchers have suggested that they produce compounds that cause branches to get sick (Cabrera, Gallo, & Seldes, 1995; Neumann, 2004). Other experts rule out this possibility, arguing that damage is inflicted differently, via competition for sunlight, excess weight, and obstruction of new shoots on affected branches (Flores-Palacios, 2016; Flores-Palacios, Barbosa-Duchateau, Valencia-Diaz, Capistran-Barradas, & Garcia-Franco, 2014; Lopez-Villalobos et al., 2008). Finally, reports on managed stands indicate that *Tire* progress on deteriorated specimens associated to age (old specimens), stress conditions due to root cutting, poor pruning, drought, insect attack or contamination, and are part of a vicious circle that ends in the tree death.

In this study, our aim was to establish whether there is a relation between the geological substrate and the degree of infestation of *Tire* and subsequently on the deterioration of infested oak trees. We hypothesized that a substrate enhancing the effects of drought, ie., shallower soil, lower fracturation in rocks, presence of low permeability layers, etc., would enhance drought effects and favor a rise in abundance of *Tillandsia* on oak canopies.

Material and Methods

The study was carried out in the mountain range of Sierra de Santa Rosa, Guanajuato, located between the coordinates 20°45'- 21°25' N and 100°53'-101°25' W, which is part of the subprovince Sierras y Llanuras del Norte de Guanajuato in the physiographic region of mesa central (Cuanalo de la Cerda & Ojeda Trejo, 1989). The geology corresponds to the cretasic period with igneous rocks such as andesites, ignimbrites, riolite, toba as well as sedimentary rocks derived from dendritic material (Cuanalo de la Cerda & Ojeda Trejo, 1989; Vega, Morrone, & Organista, 2007). The region exhibits a temperate subhumid climate with an annual average precipitation of 800 mm falling mostly in summer, with 4 to 6 months of seasonal drought (García, 2004). The mountain range presents an important humidity gradient with the northern extreme, where the experimental site is located, becoming semiarid (500 to 620 mm). The dominant vegetation type for the site is a

Quercus forest with up to 14 species and other secondary woody species from the genus: *Ageratina, Arbutus*, *Comarostaphylis* y *Solanum* (Martínez-Cruz & Téllez-Valdés, 2004; Pineda, 1978). For the forest, four main species associations have been identified, with *Quercus potosina* (*Qupo*) – *Q. castanea* (*Quca*) as the most extense, developing between 2300 and 2600 m.a.s.l. (Martínez-Cruz, Téllez Valdés, & Ibarra-Manríquez, 2009).

Rainfall variability

The data were analyzed with the objective of characterizing the pluviometric variability. Average annual rainfall regime and precipitation anomalies were calculated in the period 1980-2019 from the weather station network of the National Meteorological Service of Mexico (La Quemada-1107, San Felipe-11109, Dolores Hidalgo-11017, Guanaguato-11024, Jaral de Berrios-11030; https://smn.conagua.gob.mx/es/) and the National Network of Automated Agrometeorological Stations INIFAP (La Hacienda, Silao and El Vergel, San Felipe; https://clima.inifap.gob.mx/lnmysr/Estaciones). This analysis was also performed considering the Standardized Precipitation and Evapotranspiration Index (SPEI, Vicente-Serrano et al, 2010). The data series was obtained from the (website http:// sac.csic.es/spei/ home.html) for the period 1970-2019 at a spatial scale of 0.5º longitude and latitude. This index considers accumulated precipitation and potential evapotranspiration, making it a good indicator to study the effects of wet and dry periods on soil cover. SPEI was applied on an annual scale (12 months SPEI) and allowed characterizing the years taking into account the following criteria: +2 (extremely wet), 1.5 to 1.99 (very wet), 1.0 to 1.49 (moderately wet), -0.99 to 0.99 (normal), -1.0 to -1.49 (moderately dry), -1.5 to -1.99 (very dry), -2 (extremely dry).

Site

The study was established in the Northern distribution of Sierra de Santa Rosa, within the *Q. potosina*-*Q. castanea* association. In a forest stand exhibiting south exposition, three monitoring sites following the slope (top, middle and bottom) were set in four equidistant locations. In two of those, trees exhibited a high *Tire* infestation whereas in the other two, *Tire* was absent or observed at very low densities. To define the degree of infestation we

182 run a survey counting the number of *Tire* and their orientation in the canopy (Fig. 1). In one

183 location of the two infestation treatments (high and low *Tire* infestation), we marked 15 by

184 30 m plots. Along three transects, we inserted iron electrodes 30 cm long at 1 m distance

185 from each other at the two extremes and in the center of the plot and perpendicular to the

186 slope. The plot and electrode transect were intended for a geophysical survey and the

187 collection of plant and soil samples.

188

189 **Geophysical survey**

190 For high and low infested plots, we surveyed the subsoil using an electrical resistivity

191 tomography (ERT) method, to produce images of the variation of electrical resistivity in

192 either two or three dimensions, below a line or grid of electrodes placed on the soil surface.

193 ERT tomograms consist of a modeled cross-sectional plot of resistivity ($\Omega \cdot m-1$) versus

194 depth. The method is based on voltage difference measurements between electrodes. This is

195 a minimally invasive method; it only requires inserting electrodes a few centimeters into

196 the ground to create an electrical contact. The resulting subsurface resistivity model depicts

197 variations in the conductivity of electrical current in soil and rocks. The measured

198 resistivity is a function of the water content of the substrate (rock or soil), the chemical

199 composition of pore water and the soil surface area/grain particle size distribution. In this

200 study, to determine electric resistivity we implemented a Wenner-Schlumberger and Pole-

201 Dipolo array. Up to 96 geophysical electrodes per plot were installed with Northeast-

202 Southwest orientation and 1 m inter-electrode spacing. ERT tomograms were taken using

203 the SYSCAL KID SWITCH-24 (IRIS instruments) with a 24-multi-electrode switch box

204 Electrical resistivity tomography using a Wenner-switch array. Resistivity values were

205 corrected for the effect of temperature, based on the temperature recorded with a soil

206 thermometer at a given depth for each resistivity value, and on the Campbell equation

207 (Campbell, Bower, & Richards, 1949) as suggested by Samouëlian, Cousin, Tabbagh,

208 Bruand, and Richard (2005). Inversion and forward simulations were performed with

209 RES3DINV software (Geotomo software) for later manipulation of data files (see

210 Rodríguez-Robles *et al.* 2017), followed by 3D slicers software for layer series analysis

211 (depth: 0-30, 30-60, 60-90 and 90 to 150 cm). Tomograms were collected four times (june,

212 august, october 2016 (wet period) and november 2016, january, march and may 2017 (dry

213 period) during the study period.

214

Isotopic analysis of rainwater, dew, soil, woody and leaf tissue

216 In order to identify the role of *T. recurvata* as either epiphyte or parasite, we proceed to

217 determine all potential water sources used by *Tire* and the tree they posed on. We used a

218 sketch map of the Local Meteoric Water Line (LMWL) generated for the neighboring

219 mountain range Sierra San Miguelito (Ulises Rodríguez-Robles et al., 2020) using the $\delta^{18}O$

220 and δD values of rainwater of 52 precipitation events. To the same LMWL, 9 precipitation

221 events were added in a period of six months (06/07/16 - 11/14/16). Dew deposited on the

222 trichomes of *Tire* was collected at dawn. In addition, at monthly intervals during a year we

223 collected; *Tillandsia* crowns, twigs and trunk cores, soils (0-20, 20-40 and >40 cm) and

224 regolithic material around both species *Qupo* and *Quca*. At each sampling date from May

225 2016 – May 2017 (total = 72 samples), we collected from adult trees twigs fully covered

226 with periderm (four trees, two species) randomly selected (n = 16 twig samples per

227 sampling date, with a study total of 1152 twigs), as well as *Tillandsia* crowns. Collected

228 samples were immediately frozen with dry ice in air-tight tubes for subsequent water

229 extraction using cryogenic distillation (West, Patrickson, & Ehleringer, 2006) and posterior

230 determination of stable isotope ratios for hydrogen (D/H) and oxygen ($^{18}O/^{16}O$). The bark of

231 4 to 6 twigs 3 cm long was peeled off and the stem stored in 30-mL glass vials sealed with

232 parafilm-lined caps.

233 For stable isotope analysis, water was first extracted from soils, stems, twigs and crowns

234 through cryogenic vacuum distillation (West et al., 2006) with an extraction system

235 consisted of 8 sample tubes connected with Ultra−Torr™ fittings (Swagelok Company,

236 Solon, OH, USA) to 8 U−shaped collection tubes specifically designed for this system

237 (Martín-Gómez et al., 2015). δD and $\delta^{18}O$ values of the woody stems, twigs, soil, *Tillandsia*

238 crowns, dew and precipitation were determined using a stable isotope ratio mass

239 spectrometer (Picarro L1102-i water isotope analyzer, PICARRO, INC) at the National

240 Laboratory (LAMBAMA) located at the Instituto Potosino de Investigación Científica y

241 Tecnológica in San Luis Potosi, Mexico. Results are reported in delta values, representing

242 deviations in per mil (‰) from the Vienna Standard Mean Ocean Water 2 and Standard

243 Light Antarctic Precipitation 2 (VSMOW2/SLAP2). Overall, analytical precision of the
244 spectrometer was ±0.1‰ for $\delta^{18}O$ and ±0.6 ‰ for δD. Additionally, we used GISP
245 (International Atomic Energy Agency) and SSM2 (water-spring from Sierra de San
246 Miguelito Volcanic Complex) as two controls for quality checks in the analysis.

247 To examine the hydrological status of trees, we counted with midday leaf water potential
248 (Ψ_{leaf}) measured between 11 to 13 h t biweekly intervals from february 2014 to february
249 2016. We used psychrometric techniques and a dewpoint microvoltimeter HR-33 (Wescor
250 Inc., South Logan, UT, USA) to determine leaf water potential (C-52; Wescor Inc.). For
251 Ψ_{leaf}, we harvested three to four leaf discs from healthy mature leaves exposed to sunlight
252 and allowed 20 min for stabilization within C-52 chambers before readings.

253 To examine soil moisture content (SMC, %) was calculated by using the fresh weight
254 (Wfresh) and dry weight (Wdry) (48 hours at 70 °C) of each soil sample:

255
$$SMC = \frac{\left(\dfrac{W_{fresh}}{W_{dry}}\right)}{W_{dry}} \, x \, 100 \, \%$$

256

257 **Mixing model for the analysis of stable isotopes: relative contribution of water sources**

258 The relative contributions of different sources to xylem water (trees and epiphytes*)* were
259 estimated by a Bayesian Isotope Analysis Mixing Model (MixSAR, in R package). Stable
260 isotope mixing models are used extensively for studying food webs but they can also be
261 applied to the determination of plant water sources (Evaristo, Jasechko, & McDonnell,
262 2015; D. L. Phillips, Newsome, & Gregg, 2005). We considered five different sources of
263 water for *Quercus* including; three soil depths (0–20, 20-40 and >40 cm), regolith
264 (weathered rock) and the epiphyte. Whereas the water sources for the epiphytes we
265 considered two sources; trees (*Qupo* and *Quca*) and Dew.

266 $\delta_m^1 = f_a \delta_a^1 + f_b \delta_b^1 + f_c \delta_c^1$

267 $\delta_m^2 = f_a \delta_a^2 + f_b \delta_b^2 + f_c \delta_c^2$

268     $1 = f_a + f_b + f_c$

269   The number of sources that can be partitioned is limited by the employed number of

270   isotopic signatures. For the dual isotope example above, the mixing model is a system of

271   three equations with three unknowns (fa, fb, fc), for which there is a unique solution

272   (Donald L. Phillips & Gregg, 2003).

273   **Statistical Analysis**

274   To compare the stable isotopic composition (D/H and $^{18}O/^{16}O$ isotope ratios) considering

275   natural abundance (‰) in xylem sap of plant fractions (trunk, twigs, *Tillandsia* plants) and

276   soil water, we implemented a factorial repeated-measures analysis of variance using a

277   mixed model, which included as classification factors, species with two levels (*Q. potosina*

278   and Q. *castanea*, fixed effect), infestation level (low and high) and time (sampling dates,

279   random effect) with 26 leves (biweekly dates). Same model, varying the monitoring time

280   (15 months) was implemented to compared plant water potentials. For the water

281   redistribution analysis in *T. recuvarta,* we implemented an analysis of variance to examine

282   the deuterium excess (d-excess) of rainfall, dew, regolith water and *T. recurvata*, using a

283   mixed model with species (*Q. potosina* and *Q. castanea*, fixed effect), season (dry and wet)

284   infestation level (low and high). In all cases, we conducted Tukey's *post hoc* mean

285   comparison tests. We conducted polynomial inverse regression analyses to examine the

286   relationship between soil moisture content (SMC, %) and resistivity (ERT, $\Omega\ m^{-1}$) between

287   May 2016 and May 2017. Prior to statistical analysis we applied the Shapiro–Wilk test to

288   examine normality of the residuals. Spatial analysis of soil electrical resistivity at different

289   soil depths (0-30, 30-60, 60-90 and 90-150 cm) were examined using the Kriging

290   interpolation method (Empirical Bayesian Kriging Simulations). All geostatistical analyses

291   were run with ArcGIS v. 10.5 for Windows (ArcGIS Desktop, ESRI 2018). The relative

292   contributions of different sources to xylem water were estimated with MixSIAR package

293   (Bayesian isotope analysis mixing model in R)

294   https://cran.r-project.org/web/packages/MixSIAR/

295

296   **Results**

297   **Analysis of rainfall trends and dry periods**

298   The pluviometric analysis showed a historical average rainfall of 780 mm, presenting a
299   reduction of ~ 17% (-130 mm anomaly) for the last 10 years and a decrease of ~ 26% (-201
300   mm anomaly) for the last 5 years (Fig. S1, top). The months from may to october are the
301   ones presenting the greater rainfall reduction (25%, average), with june and august showing
302   anomalies of up to -32% (Fig. S1, bottom). February is the only month presenting a
303   positive anomaly of + 72% (24 mm, average). The highest precipitation recorded
304   corresponds to 2007 with a pluviometric anomaly of +510 mm. Four markedly dry years
305   were observed with anomalies of -390 mm (1996), -486 mm (1999), -424 mm (2012) and -
306   583 mm (2013), the year 2013 being extremely dry. In the analysis of SPEI index we
307   observed more humid years (27) than dry ones (23) within a period of 50 years. Three very
308   humid periods were also observed (SPEI +1.65; 1973-76, 1991-95 and 2006-14) as well as
309   two years with extreme humidity (SPEI +2; 1993 and 2010). Drought trends are well
310   marked for Sierra de Santa Rosa, as well three very humid periods with values above +1.55
311   SPEI (1977-82, 1984-85 1997-2002) and one extremely dry period (SPEI -2; 2011-13),
312   2013 being the record dry year (SPEI -2.63). Our 13-month study occurred during a
313   moderately dry period (SPEI -0.85 average).
314

Time-lapse ERT survey: wet and dry season

316   We examined the relationship between electrical resistivity and soil moisture content,
317   observing higher moisture content values corresponding with low soil resistivity values ($P>$
318   0.001, $R^2= 0.58$). The color gradient along the soil profile (0-150 cm depth) depicts regions
319   of soil humidity, with high content in blue (65% soil moisture content, SMC, 37 $\Omega \cdot$ m)
320   towards low humidity regions in red (15% SMC, $\geq 695 \Omega \cdot$ m) (Figs. 3 and 4). Before, we
321   monitored *Tillandsia* density on trees in several places to identify plots with low and high
322   *Tire* presence. Sites with low *Tire* density were restricted to only one quadrant of the tree
323   canopy (Fig. 1a) compared to high density plots were *Tire* occupied the whole canopy (Fig.
324   1b). Also, there were significant differences in Tire number depending on *Quercus* species
325   and density. Thus, *Quca* exhibited 48±15.3 and 16±6.2, while *Qupo* presented 39±11.2 and
326   109±33.4 low and high density respectively.
327

High infestation site

329 We observed significant differences between wet and dry seasons for the mean ERT

330 tomogram values (P <0.001; 287.24 ± 23 vs 616 ± 82.42, for wet and dry respectively). We

331 observed that *Qupo* trees (circles) were distributed over the regolithic material while *Qrec*

332 (crosses) were established on top of infiltration regions (Figs. 2a, b). In the wet season

333 occurring between june and october 2016, the 3D-slicer at 0-30 cm depth, presented the

334 lowest resistivity values (average 125 $\Omega \cdot$ m) corresponding to ~24% SMC. Along the soil

335 profile, we identified a dryness gradient, observing with the 3D-slicer between 90 to 150

336 cm depth the highest resistivity values ($\geq$ 695 $\Omega \cdot$ m), however they were associated to

337 highly defined regions of SMC $\geq$ 60% (88 a 37 $\Omega \cdot$ m) (Fig. 2a) corresponding to

338 infiltration regions (*i.e.* fractures).

339 For the dry season in the high infestation plots, between november 2016 and may 2017,

340 recorded resistivity values of 285 to 617 $\Omega \cdot$ m (18 to 16% SMC) were observed for the

341 first 30 cm of soil (Fig. 3a). The 3D-slicer corresponding to the 60 to 90 cm layer showed

342 the highest resistivities in the ERT tomogram with values $\geq$ 695 $\Omega \cdot$ m. Whereas, the 3D-

343 slicer for the 90-150 cm layer was the one presenting regions with the lowest values $\leq$ 37 Ω

344 $\cdot$ m with well-defined humidity regions (blue color). Infiltration regions are observed along

345 the soil depth gradient, ranging from dry-green in the upper slice to blue in the lower slicer

346 (X axis: 10 to 30 m, Y axis: 0 to 10, a central region). The regions from orange to red are

347 the areas where it is spatially distributed the regolithic material (weathered rock).

348

349 **Low infestation sites**

350 In the site with low *Tire* infestation, there was no significant differences between the wet

351 and dry periods for the mean ERT-3D Slicer Tomogram values (P< 0.05; 286.17 ±21 $\Omega \cdot$m

352 wet season vs 315.81 ±105 $\Omega \cdot$m dry season, respectively). For the wet season, regions of

353 very low resistivity (37 to 145 $\Omega \cdot$ m) were observed within the first 90 cm of depth where

354 infiltration regions are observed in blue and showing in yellow the regions where

355 weathered material predominates (Fig. 2b). The superficial 3D-slicer also exhibited spatial

356 variability for the SMC (17 to 65%). Tree positions in the plot for both *Qupo* and *Quca* are

357 related to areas with low resistivity (45 to 175 $\Omega \cdot$ m) in particular the 60 to 90 cm layer.

358 This layer in the wet season showed the highest SMC, with a 72% of blue area

359 corresponding to ~ 44% SMC ($\leq$ 37 $\Omega \cdot$ m), whereas regions in yellow and red indicate the

360   presence of regolithic material. Regolithic material with no or very low humidity (≥ 695 Ω

361   · m) neighboring soil of very low humidity (≥ 275 Ω · m) was observed in the 90-150 cm

362   3D-slicer.

363   For the dry season, all 3D-slicers showed higher resistivities, for instance 0-30 and 90-150

364   cm 3D-slicers showed predominant values between 550 to 725 Ω · m. The layer from 60-

365   90 cm distinguished from the others by the very heterogeneous SMC and resistivity values,

366   marking very abundant regions of humidity (18% SMC, ≤ 33 Ω · m) (Fig. 3b).

367

368   **Geospatial and temporal water use**

369   The geologic substrate in the oak forest from Sierra de Santa Rosa is characterized by

370   regolithic materials (weathered rock) which is distributed along the ground profile (0-150

371   cm depth). The regolith isotopic signatures in our collecting site were $\delta^{18}O$ -5.88 $\pm$ 1 ‰ and

372   δD -65.94 $\pm$ 11 ‰, while the mean isotopic signatures for the soil were $\delta^{18}O$ -7.32 $\pm$ 3 ‰

373   and δD -75.8 $\pm$ 32 ‰. On the other hand, the natural abundance of dew ranges from $\delta^{18}O$ -

374   10.35, δD -114.27 ‰ to $\delta^{18}O$ -9.17 ‰, δD 99.11 ‰ (Fig. 4.1b).

375   Sites with high *Tire* infestation showed significant difference in xylem isotopic signal

376   respect to low infestation (P <0.001, Fig. 4.1, 4.2, 4.3), as well as season (wet and dry, P

377   <0.001, Fig. 4.1, 4.2, 4.3). Also, *Qupo* and *Quca* showed significantly different isotopic

378   signatures (P <0.04), with *Qupo* exhibiting the most impoverished isotopic signatures

379   during the dry season (*Qupo* = $\delta^{18}O$ - 9.1 $\pm$ 2 ‰, δD -92.16 $\pm$ 34 vs *Quca* = $\delta^{18}O$ - 7.14 $\pm$ 2

380   ‰, δD -81.22 $\pm$ 11) and for sites with high infestation ($\delta^{18}O$ - 8.7 $\pm$ 4 ‰, δD -87.33 $\pm$ 37

381   ‰, respect). During the dry season, both *Qupo* and *Quca* used stored water from the

382   regolith (Fig. 4.1a-b, 4.3a-f, 4.4a-f), contributing with ~ 33% in *Qupo* and ~ 40% in *Quca*

383   of their water demand (Fig. 5 bottom). Whereas in the rainy season, the regolith contributed

384   with up to 35% of the water for *Quca*, and less than 10% for *Qupo* (Fig. 5 top).

385   Since *Tillandsia* acquires water from the atmosphere, we use *Tire* isotopic water values as a

386   source indicator of atmospheric humidity. We observed that the highly infested *Qupo* in the

387   dry season presented *Tire* isotopic water values for up to 22% (Figs. 5, 4.1b, 4.2f, 4.3b, d,

388   4.4b), whereas in the rainy season *Tire* contributed with ~ 13% (Fig. 4.1d, f, h, 4.2b, d),

389   decreasing at the same time the water used from the regolith (~ 7%). In the rainy season,

390   for *Qupo* and *Quca* at both infestation sites, the main water source was the 0-30 cm soil

391   profile (~33%) while in the dry season it was from the regolithic material (~35%). For the

392   relative contribution of water sources to *Tire*, we examined dew and xylem water from

393   trees as sources. During the rainy season *Quca* was a source of water to *Tire* contributing

394   with up to 17% of its water demand in the high infestation site. The contribution by *Qupo*

395   was less than 7% and in sites with low infestation (Fig. 6), while *Qupo* did not contributed

396   as a water source in the wet season when *Tire* only depended on dew (100%). During the

397   dry season, the water contributions by the two species began to be more important, with

398   *Qcat* contributing ~ 34% and *Qupo* 14%, while in the low infestation site, *Qupo* contributes

399   only ~ 6% of *Tire* water demand. Thus, for the high infestation site, *Tire* isotopic signatures

400   established on *Quca* were similar to *Quca* twigs water, both of them showing values above

401   the local meteorological water line (Fig 4.1b, d, f, h, 4.2d).

402

403   **Distribution of *d*-exccess in rainfall, dew and *Tillandsia recurvata***

404   Deuterium excess (*d-excess*) values in precipitation indicate changes in the conditions at the

405   moisture sources and recycling processes along the moisture tracks (Chakraborty, Belekar,

406   Datye, & Sinha, 2018). These differences are clearly discernible when identifying the

407   moisture sources based on the analysis of *d-excess* values of precipitation water (Araguás-

408   Araguás, Froehlich, & Rozanski, 2000). Mean and standard deviations of rainfall, dew and

409   *Tire* values were 2.45 ±2.4 ‰, -29.82 ±2.73 ‰ and -15.53 ±0.98 ‰, respectively. We

410   identified *d-excess* significant differences for *Tire* between sites and season (P <0.001),

411   showing lower *d-excess* values for the site with low compared to high infestation (-20.938

412   ± 1.02 ‰ vs -7.594 ± 1.02 ‰, Fig. S2) and during the dry compared to the wet season (-

413   19,365 ± 0.977 ‰ vs -9.167 ± 1.07 ‰). The range of *d-excess* values shown on the gray

414   band (-34.4 ‰ to -24.2 ‰, Fig. S2) are the result of enhanced evaporation through

415   processes such as dew formation, while the values of rainfall are close to the Meteorical

416   Water Line, *d*-excess ± 10 ‰.

417

418   **Discussion**

419   Symptoms of either decaying or mortality in forest are frequently reported to occur as spots

420   within the forest matrix (Allen et al., 2010; Nate McDowell et al., 2018). A reason for this

421   pattern might be related to the variability in the substrate sustaining the forest, the

geodiversity (Brantley et al., 2017). Differences in soil depth, rock outcropping, rock fracturing, fracture depth, etc., may affect the hydrology at specific sites (Rodriguez Robles et al., 2020). These geologic differences may subsequently set conditions in terms of exposing trees to divergent degrees of drought and levels of stress. Sites imposing greater stress may weaken tree condition affecting for instance, the synthesis of secondary compounds for defense and becoming more susceptible to diseases and pest invasion. In this way, sites exhibiting a geodiversity that reduces water storage may harbor tree stands showing decay, mortality or just greater susceptibility to climatic variability.

In this study, we presented evidence that differences in geodiversity are likely related to *Tillandsia recurvata* infestation. Thus, when comparing infestation sites, it was clear that high infestation sites coincided with substrates showing the highest resistivity at lower depths. For instance, during the wet season the high infestation site showed higher resistivities than low infestation already at the 30 – 60 cm layer (Fig. 2a). These high resistivities almost predominate in the layer from 60 – 90 cm whereas, in the low infestation site this layer is still dominated by very low resistivities (ci. 37 $\Omega \cdot$ m, Fig. 2b). During the dry season, high resistivities were observed at the top layer (0 - 30 cm) in both the high and the low infestation sites, however in the low infestation resistivities decreased in the following layer (30 – 60), indicating greater water availability. The high infestation remained with similar high resistivities as the top in the 30 to 60 cm layer and increased to the highest in the 60 – 90 cm depth (695 $\Omega \cdot$ m, Fig. 2a).

As mentioned before, resistivities depended on the structural components of a particular substrate layer, therefore in the wet season the recorded high resistivities were a consequence of the predominance of regolith and rocks with different degrees of fracturation. This distinctive differences in geodiversity imply different hydrologic routes, water holding capacities and imposition of drought conditions affecting tree stands performance. It is very likely that the more limiting geologic conditions for the vegetation likely contributed to lower water availability as corroborated by the soil water content (Figs. 2, 3) and the leaf water potential (Fig. S3). This, may eventually weakened the forest stand, allowing the increase of *Tire* population densities on trees (Fig. 1b). One hypothesis suggests that the weakening of tree condition would emerge as a consequence of a lower substrate humidity and long-lasting stress in sites with predominance of regolith and rocks

453   (high infested, Anderegg *et al.* 2015). As a result, under these humidity conditions, trees

454   may reduce the synthesis of secondary compounds for defense becoming more susceptible

455   to pest's infestation (Landhäusser & Lieffers, 2012; Sala, 2009). This might be the case for

456   *Tillandsia* success in infesting oak at this forest.

457   Once installed on the tree, *Tire* apparently switched from an epiphytic to a parasitic plant.

458   For instance, Pérez-Noyola et al. (2020) reported that *Tire* becomes what they called "a

459   structural parasite" on mezquite (*Prosopis laevigata*), since *Tire* ryzoids are capable to

460   penetrate mezquite's bark reaching and blocking its vascular conducts, however this work

461   did not reveal uptake from tree resources. This appears to be the case in oak, but

462   additionally our results revealed that *Tire* used not only dew (gray band, Fig. 8) but also

463   oak xylem water, with *Quca* contributing with up to 34% of *Tillandsia* water demand

464   during the dry season in the high infestation site (Fig. 4.4d, f). At least in infested *Quca,*

465   *Tillandsia* used tree water along the whole year.

466   With *Tillandsia* taking water from the tree, we expected to observe infested trees under a

467   greater water stress than low infested trees, however the opposite observation was the rule.

468   Using, leaf water potentials from both infestation treatments we noticed that trees from high

469   infestation sites presented less negative average values than low infestation trees (-1.39 vs.

470   -

471   1.54 MPa respectively, Fig. S3). Further examination showed that this result coincided with

472   the observation that *Tillandsia* functions as a source of water for both oaks, in particular for

473   *Qupo* that acquired up to 22% of its water demand during the drought period and high

474   infestation conditions (Fig. 5). It appears that the lower plant water potentials of both oak

475   species under high infestation conditions may have resulted from *Tire* acting as a via to

476   acquire atmospheric water by oak. This suggest that the observed decay in the high infested

477   trees might not only be the result of *Tire* high densities but perhaps from either a

478   predisposition to the attack by pests including fungus, bacteria and insects on weakened

479   trees or from the fact that *Tillandsia* plants might also profit from assimilates produced by

480   oak trees throughout the invagination of tree vascular bundles.

481   It is well known that pests and other forest pathogens contribute to the process of forest

482   mortality under drought conditions. Many fungi and insects, for example, attack weakened

483   trees by drought, accelerating their death (Desprez-Loustau, Marçais, Nageleisen, Piou, &

484 Sci., 2006; Jactel et al., 2012; Martínez-Vilalta, Lloret, & Breshears, 2012). In the first

485 case, the presence of fungi of the genus *Phytophthora* which is considered the most

486 important pathogen of woody plants, causes massive death of roots in oak forests, hence

487 reducing tree's capability for water uptake and nutrient capture (N. G. McDowell, 2011;

488 Sevanto, McDowell, Dickman, Pangle, & Pockman, 2014). It has also been reported that

489 *Phytophthora* causes foliar symptoms similar to those of drought, *i.e.* necrotizing leaves

490 and cracking branches. Throughout tree inspections at the site, we identified these same

491 symptoms in leaves and branches, as well as fruiting bodies at the base of trunks, including

492 *Tire* penetrating the bark and cracks in branches. We hypothesize that pathogenic fungi

493 could open the way to the incursion of *Tire* roots into tree conductive system. Thus, *Tire*

494 could forage water and solutes when the tree is weakened by pathogens that also feed on

495 carbon and nutrients from the living cells, damaging the tree tissues that carry out

496 carbohydrates, while triggering a tree defensive response (Oliva, Stenlid, & Martínez-

497 Vilalta, 2014). This response is based on investing many sugars to produce defensive

498 secondary compounds, likely contributing to trees death by starvation. As a second

499 hypothesis, in a stressful environment, *Tire*, through its rhizoids, could be releasing

500 hydroperoxycycloartan compounds that acts as an antibiotic (allelopathic) causing bud

501 death and foliage abscission (Neumann, 2004). This could explain branches death due to a

502 vicious cycle of increased colonization - more shade - more allelopathic effect - fewer buds

503 - less foliage for photosynthesis.

504 In terms of photo-assimilates uptake by *Tire*, it has already being established that some

505 stem hemiparasites such as cuscuta, mistletoes, etc.; even though they present

506 photosynthesis, still they capture organic carbon from the host xylem (Bell & Adams, 2011;

507 Těšitel, 2016). The importance of taking up these assimilates from the host become more

508 relevant when the hemiparasite own photosynthesis is limited by either reduced light

509 incidence or mineral nutrient deficiency (Těšitel, Těšitelová, Fisher, Lepš, & Cameron,

510 2015). *Tillandsia recurvata* is a monocot belonging to the *Bromeliaceae* that are overall

511 considered epiphytic plants. These are generally plants of approximately 5-15 cm high,

512 which grows on trees and shrubs, although also on the power lines and rocks. Its leaves are

513 grayish recurved, and present terminal inflorescence, generally with one or five flowers. At

514 the biogeographic level, it is distributed in tropical and subtropical countries, including

515 Mexico (Bernal, Valverde, & Hernandez-Rosas, 2005). Part of its success to get established
516 on several surfaces relates to its capacity to fix atmospheric nitrogen and its CAM
517 photosynthetic pathway (Diaz-Alvarez, de la Barrera, Barrios-Hernandez, & Arroniz-
518 Crespo, 2020; Victoriano-Romero et al., 2020). Although, *Tillandsia* appears to function as
519 a hemiparasitic plant, these previous characteristics suggest that *Tire* may not suffer of
520 insufficient photosynthesis and lack of nitrogen to be forced to acquire host assimilates.
521 Still, this is an issue that requires to be investigated.

522 In conclusion, this study shows that the structural composition of the substrate (*i.e.*
523 geodiversity) may impose different conditions of water availability to forest. This, together
524 with the annual climatic variability may enhance drought stress conditions that weaken tree
525 forest allowing the infestation by *Tillandsia* and likely pathogenic fungus. The rise in
526 temperatures may also play an additional role of *Tire* infestation since its presence in
527 mountain ecosystems occurred within the last decade. *Tire* maintains a tropical and
528 subtropical distribution however it is very likely that warmer temperatures will allow *Tire*
529 to expand its distribution range into higher altitudes.

530

531 **Author Contributions**
532 URR and TA contributed equally**:** Conceptualization, Methodology, Formal analysis,
533 Writing - review & editing and Funding acquisition.

534

535 **Declaration of competing interest**
536 The authors declare that they have no known competing financial interests or personal
537 relationships that could have appeared to influence the work reported in this paper.

538

539 **Data Availability Statement**
540 We declare the data that support the findings of this study are available from the
541 corresponding author upon reasonable request.

542

References

Aguilar-Rodríguez, S., Terrazas, T., Huidobro-Salas, M. E., & Aguirre-León, E. (2016). Anatomical and histochemical bark changes due to growth of Tillandsia recurvata (ball moss). *J Botanical Sciences, 94*, 551-562.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., . . . Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management, 259*(4), 660-684. doi:http://dx.doi.org/10.1016/j.foreco.2009.09.001

Anderegg, W. R., Hicke, J. A., Fisher, R. A., Allen, C. D., Aukema, J., Bentz, B., . . . Zeppel, M. (2015). Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytol, 208*(3), 674-683. doi:10.1111/nph.13477

Araguás-Araguás, L., Froehlich, K., & Rozanski, K. (2000). Deuterium and oxygen-18 isotope composition of precipitation and atmospheric moisture. *14*(8), 1341-1355. doi:10.1002/1099-1085(20000615)14:8<1341::Aid-hyp983>3.0.Co;2-z

Bell, T. L., & Adams, M. A. (2011). Attack on all fronts: functional relationships between aerial and root parasitic plants and their woody hosts and consequences for ecosystems. *Tree Physiol, 31*(1), 3-15. doi:10.1093/treephys/tpq108

Bernal, R., Valverde, T., & Hernandez-Rosas, L. (2005). Habitat preference of the epiphyte Tillandsia recurvata (Bromeliaceae) in a semi-desert environment in Central Mexico. *Canadian Journal of Botany-Revue Canadienne De Botanique, 83*(10), 1238-1247. doi:10.1139/b05-076

Bigler, C., Bräker, O. U., Bugmann, H., Dobbertin, M., & Rigling, A. (2006). Drought as an Inciting Mortality Factor in Scots Pine Stands of the Valais, Switzerland. *Ecosystems, 9*(3), 330-343. doi:10.1007/s10021-005-0126-2

Brantley, S. L., McDowell, W. H., Dietrich, W. E., White, T. S., Kumar, P., Anderson, S. P., . . . Gaillardet, J. (2017). Designing a network of critical zone observatories to explore the living skin of the terrestrial Earth. *Earth Surf. Dynam., 5*(4), 841-860. doi:10.5194/esurf-5-841-2017

Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann. For. Sci., 63*(6), 625-644.

Cabrera, G. M., Gallo, M., & Seldes, A. M. (1995). A 3,4-seco-cycloartane derivative from Tillandsia usneoides. *Phytochemistry, 39*(3), 665-666. doi:https://doi.org/10.1016/0031-9422(95)00076-J

Campbell, R. B., Bower, C. A., & Richards, L. A. (1949). Change of Electrical Conductivity With Temperature and the Relation of Osmotic Pressure to Electrical Conductivity and Ion Concentration for Soil Extracts. *13*(C), 66-69. doi:10.2136/sssaj1949.036159950013000C0010x

Chakraborty, S., Belekar, A. R., Datye, A., & Sinha, N. (2018). Isotopic study of intraseasonal variations of plant transpiration: an alternative means to characterise the dry phases of monsoon. *Scientific Reports, 8*(1), 8647. doi:10.1038/s41598-018-26965-6

Cortes-Anzures, B. O., Corona-Lopez, A. M., Toledo-Hernandez, V. H., Valencia-Diaz, S., & Flores-Palacios, A. (2017). Branch mortality influences phorophyte quality for vascular epiphytes. *Botany, 95*(7), 709-716. doi:10.1139/cjb-2017-0023

Cuanalo de la Cerda, H. E., & Ojeda Trejo, E. (1989). *Provincias regiones y subregiones terrestres de México*. Retrieved from

590 Desprez-Loustau, M.-L., Marçais, B., Nageleisen, L.-M., Piou, D., & Sci., A. V. J. A. F. (2006).
591   Interactive effects of drought and pathogens in forest trees. *63*(6), 597-612.
592 Diaz-Alvarez, E. A., de la Barrera, E., Barrios-Hernandez, E. Y., & Arroniz-Crespo, M. (2020).
593   Morphophysiological screening of potential organisms for biomonitoring nitrogen
594   deposition. *Ecological Indicators*, *108*. doi:10.1016/j.ecolind.2019.105729
595 Dietze, M. C., & Matthes, J. H. (2014). A general ecophysiological framework for modelling the
596   impact of pests and pathogens on forest ecosystems. *17*(11), 1418-1426.
597   doi:10.1111/ele.12345
598 Evaristo, J., Jasechko, S., & McDonnell, J. J. (2015). Global separation of plant transpiration from
599   groundwater and streamflow. *Nature*, *525*(7567), 91-94. doi:10.1038/nature14983
600 Flores-Palacios, A. (2016). Does structural parasitism by epiphytes exist? A case study between
601   Tillandsia recurvata and Parkinsonia praecox. *Plant Biology*, *18*(3), 463-470.
602   doi:10.1111/plb.12406
603 Flores-Palacios, A., Barbosa-Duchateau, C. L., Valencia-Diaz, S., Capistran-Barradas, A., & Garcia-
604   Franco, J. G. (2014). Direct and indirect effects of Tillandsia recurvata on Prosopis laevigata
605   in the Chihuahua desert scrubland of San Luis Potosi, Mexico. *Journal of Arid
606   Environments*, *104*, 88-95. doi:10.1016/j.jaridenv.2014.02.010
607 García, E. (2004). *Modificaciones al sistema de clasificación climática de Köppen*: Universidad
608   Nacional Autónoma de México.
609 Gray, M. (2004). *Geodiversity: Valuing and Conserving Abiotic Nature*: Wiley.
610 Hartmann, H., Adams, H. D., Anderegg, W. R. L., Jansen, S., & Zeppel, M. J. B. (2015). Research
611   frontiers in drought-induced tree mortality: crossing scales and disciplines. *205*(3), 965-
612   969. doi:10.1111/nph.13246
613 Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A., & Koricheva, J. (2012).
614   Drought effects on damage by forest insects and pathogens: a meta-analysis. *18*(1), 267-
615   276. doi:10.1111/j.1365-2486.2011.02512.x
616 Landhäusser, S. M., & Lieffers, V. J. (2012). Defoliation increases risk of carbon starvation in root
617   systems of mature aspen. *Trees*, *26*(2), 653-661. doi:10.1007/s00468-011-0633-z
618 Lopez-Villalobos, A., Flores-Palacios, A., & Ortiz-Pulido, R. (2008). The relationship between bark
619   peeling rate and the distribution and mortality of two epiphyte species. *Plant Ecology*,
620   *198*(2), 265-274. doi:10.1007/s11258-008-9402-5
621 Martín-Gómez, P., Barbeta, A., Voltas, J., Peñuelas, J., Dennis, K., Palacio, S., . . . Ferrio, J. P. (2015).
622   Isotope-ratio infrared spectroscopy: a reliable tool for the investigation of plant-water
623   sources? , *207*(3), 914-927. doi:10.1111/nph.13376
624 Martínez-Cruz, J., & Téllez-Valdés, O. J. B. S. (2004). Listado florístico de la sierra de Santa Rosa,
625   Guanajuato, México. *Botanical Sciences*(74), 31-49.
626 Martínez-Cruz, J., Téllez Valdés, O., & Ibarra-Manríquez, G. J. R. m. d. b. (2009). Estructura de los
627   encinares de la sierra de Santa Rosa, Guanajuato, México. *80*(1), 145-156.
628 Martínez-Vilalta, J., Lloret, F., & Breshears, D. D. (2012). Drought-induced forest decline: causes,
629   scope and implications. *Biol Lett*, *8*(5), 689-691. doi:10.1098/rsbl.2011.1059
630 McDowell, N., Allen, C. D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chambers, J., . . . Xu, X.
631   (2018). Drivers and mechanisms of tree mortality in moist tropical forests. *219*(3), 851-
632   869. doi:10.1111/nph.15027
633 McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., . . . Yepez, E. A.
634   (2008). Mechanisms of plant survival and mortality during drought: why do some plants
635   survive while others succumb to drought? *New Phytol*, *178*(4), 719-739.
636   doi:10.1111/j.1469-8137.2008.02436.x

637 McDowell, N. G. (2011). Mechanisms linking drought, hydraulics, carbon metabolism, and
638   vegetation mortality. *Plant Physiol, 155*(3), 1051-1059. doi:10.1104/pp.110.170704
639 Meddens, A. J. H., Hicke, J. A., Macalady, A. K., Buotte, P. C., Cowles, T. R., & Allen, C. D. (2015).
640   Patterns and causes of observed piñon pine mortality in the southwestern United States.
641   *206*(1), 91-97. doi:10.1111/nph.13193
642 Netherer, S., Matthews, B., Katzensteiner, K., Blackwell, E., Henschke, P., Hietz, P., . . . Schopf, A.
643   (2015). Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New*
644   *Phytol, 205*(3), 1128-1141. doi:10.1111/nph.13166
645 Neumann, R. (2004). *Clavel de aire, un parásito estructural y su control*. Retrieved from
646   http://anterior.inta.gov.ar/salta/info/boletines/desideratum/boletin_desideratum17.htm
647 Oliva, J., Stenlid, J., & Martínez-Vilalta, J. (2014). The effect of fungal pathogens on the water and
648   carbon economy of trees: implications for drought-induced mortality. *203*(4), 1028-1035.
649   doi:10.1111/nph.12857
650 Pérez-Noyola, F. J., Flores, J., Yáñez-Espinosa, L., Jurado, E., González-Salvatierra, C., & Badano, E.
651   (2020). Is ball moss (Tillandsia recurvata) a structural parasite of mesquite (Prosopis
652   laevigata)? Anatomical and ecophysiological evidence. *Trees*. doi:10.1007/s00468-020-
653   02023-5
654 Phillips, D. L., & Gregg, J. W. (2003). Source partitioning using stable isotopes: coping with too
655   many sources. *Oecologia, 136*(2), 261-269. doi:10.1007/s00442-003-1218-3
656 Phillips, D. L., Newsome, S. D., & Gregg, J. W. (2005). Combining sources in stable isotope mixing
657   models: alternative methods. *Oecologia, 144*(4), 520-527. doi:10.1007/s00442-004-1816-8
658 Pineda, R. J. B. y. F. (1978). La vegetación forestal del estado de Guanajuato. *1*, 31-41.
659 Raffa, K. F., Aukema, B. H., Bentz, B. J., Carroll, A. L., Hicke, J. A., Turner, M. G., & Romme, W. H.
660   (2008). Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification:
661   The Dynamics of Bark Beetle Eruptions. *BioScience, 58*(6), 501-517. doi:10.1641/B580607
662 Rodríguez-Robles, U., Arredondo, J. T., Huber-Sannwald, E., Yépez, E. A., & Ramos-Leal, J. A.
663   (2020). Coupled plant traits adapted to wetting/drying cycles of substrates co-define niche
664   multidimensionality. *Plant Cell Environmental, 43*(10). doi:10.1111/pce.13837
665 Rodríguez-Robles, U., Arredondo, T., Huber-Sannwald, E., Ramos-Leal, J. A., & Yépez, E. A. (2017).
666   Technical note: Application of geophysical tools for tree root studies in forest ecosystems
667   in complex soils. *Biogeosciences, 14*, 5343-5357. doi:10.5194/bg-14-5343-2017
668 Sala, A. (2009). Lack of direct evidence for the carbon-starvation hypothesis to explain drought-
669   induced mortality in trees. *106*(26), E68-E68. doi:10.1073/pnas.0904050106 %J
670   Proceedings of the National Academy of Sciences
671 Samouëlian, A., Cousin, I., Tabbagh, A., Bruand, A., & Richard, G. (2005). Electrical resistivity survey
672   in soil science: a review. *Soil and Tillage Research, 83*(2), 173-193.
673   doi:https://doi.org/10.1016/j.still.2004.10.004
674 Sevanto, S., McDowell, N. G., Dickman, L. T., Pangle, R., & Pockman, W. T. (2014). How do trees
675   die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant Cell Environ,*
676   *37*(1), 153-161. doi:10.1111/pce.12141
677 Těšitel, J. (2016). Functional biology of parasitic plants: a review. *Plant Ecology and Evolution,*
678   *149*(1), 5-20. doi:10.5091/plecevo.2016.1097
679 Těšitel, J., Těšitelová, T., Fisher, J. P., Lepš, J., & Cameron, D. D. (2015). Integrating ecology and
680   physiology of root-hemiparasitic interaction: interactive effects of abiotic resources shape
681   the interplay between parasitism and autotrophy. *205*(1), 350-360.
682   doi:10.1111/nph.13006

683 van Mantgem, P. J., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fulé, P. Z., . . .
684   Veblen, T. T. (2009). Widespread Increase of Tree Mortality Rates in the Western United
685   States. *Science, 323*(5913), 521-524. doi:10.1126/science.1165000
686 Vega, I. L., Morrone, J. J., & Organista, D. E. (2007). B5 Biodiversidad de la Faja Volcánica
687   Transmexicana.
688 Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A Multiscalar Drought Index
689   Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index.
690   *Journal of Climate, 23*(7), 1696-1718. doi:10.1175/2009JCLI2909.1 %J Journal of Climate
691 Victoriano-Romero, E., Garcia-Franco, J. G., Mehltreter, K., Valencia-Diaz, S., Toledo-Hernandez, V.
692   H., & Flores-Palacios, A. (2020). Epiphyte associations and canopy soil volume: nutrient
693   capital and factors influencing soil retention in the canopy. *Plant Biology, 22*(3), 541-552.
694   doi:10.1111/plb.13080
695 West, A. G., Patrickson, S. J., & Ehleringer, J. R. (2006). Water extraction times for plant and soil
696   materials used in stable isotope analysis. *Rapid Commun Mass Spectrom, 20*(8), 1317-
697   1321. doi:10.1002/rcm.2456

698   **Figure captions**

699

700   **Figure 1.** Plant density of *Tillandsia recurvata* and their orientation in the canopy for, **a)**
701   low and **b)** high infestation.

702   **Figure 2.** 3D-ETR slicer tomograms in mixed oak plots (*Q. potosina* and *Q. castanea*) with
703   **a)** high and **b)** low *T. recurvata* infestation during the rainy season. The 3D slicer shows the
704   relationship between soil resistivity (ohm meter) and moisture content water (MCW) at
705   every 30 cm depth, except the last layer that is 60 cm depth. Symbols indicate the presence
706   of oak trees, with circles corresponding to *Qupo* and crosses to *Quca*.

707   **Figure 3.** 3D-ETR slicer tomograms in mixed oak plot (*Q. potosina* and *Q. castanea*) with
708   **a)** high and **b)** low *T. recurvata* infestation during the dry season. The 3D slicer shows the
709   relationship between soil resistivity (ohm, meter) and moisture content water (MCW) at
710   every 30 cm depth, except the last layer that is 60 cm depth. Symbols indicate the presence
711   of oak trees, with circles corresponding to *Qupo* and crosses to *Quca*.

712   **Figure 4.1.** δ^2H and δ^{18}O isotopic composition of xylem sap (trunk, twig and *Tire*) of both
713   *Quercus potosina* and *Quercus Castanea* as well as soil water in mixed forest plots
714   presenting low and high *Tire* infestation. The different panels show the water source
715   determined in xylem water between May and August 2016: (**a, b**) May, (**c, d**) June, (**e, f**)
716   July, (**g, h**) August.

717   **Figure 4.2.** δ^2H and δ^{18}O isotopic composition of xylem sap (trunk, twig and *Tire*) of both
718   *Quercus potosina* and *Quercus Castanea* as well as soil water in mixed forest plots
719   presenting low and high *Tire* infestation. The different panels show the water source
720   determined in xylem water between September and November 2016; (**a, b**) September, (**c,**
721   **d**) October, (**e, f**) November.

722   **Figure 4.3.** δ^2H and δ^{18}O isotopic composition of the xylem sap (trunk, twig and *Tire*) of
723   both *Quercus potosina* and *Quercus Castanea* as well as soil water in mixed forest plots
724   presenting low and high *Tire* infestation. The different panels show the water source
725   determined in xylem water between December 2016 and February 2017; (**a, b**) December,
726   (**c, d**) January, (**e, f**) February.

727 **Figure 4.4.** δ^2H and $\delta^{18}O$ isotopic composition of the xylem sap (trunk, twig and *Tire*) of
728 both *Quercus potosina* and *Quercus Castanea* as well as soil water in mixed forest plots
729 presenting low and high *Tire* infestation. The different panels show the water source
730 determined in xylem water between March and May 2017; (**a, b**) March, (**c, d**) April, (**e, f**)
731 May.

732 **Figure 5.** Relative mean contribution of soil water sources and *Tire* water identified from
733 xylem water extracted from oak (*Qupo* and *Quca*) exhibiting low and high *Tire* infestation
734 during the rainy (**top**) and dry (**bottom**) seasons. Xylem water was obtained from five
735 plants and the contribution of each source was obtained through MixSIAR Bayesian
736 models. Soil layers include; H1: upper soil layer between 0–20 cm, H2: lower soil layer
737 between 20–40 cm and H3: groundwater (below 40 cm).

738 **Figure 6.** Relative mean contribution of dew and tree xylem water as sources for *Tillandsia*
739 *recurvate* posed on oak (*Qupo* and *Quca*) with low and high infestation during the rainy
740 (**top**) and dry (**bottom**) seasons. The contribution of each source was obtained through
741 MixSIAR Bayesian models.