

Indirect facilitation by a liana might explain the dominance of a small tree in a temperate forest

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Abstract

Aims

Lianas are expected to influence composition, structure and functioning of forest systems due to unequal distribution across the potential set of host plants. However, our understanding of mechanisms associated with preferences for specific hosts is still limited, and so is our ability to discern between endogenous and exogenous forces driving forest dynamics in the long run. In this paper, we evaluated whether the dominant liana *Hedera helix* can indirectly contribute to the eventual dominance of the small multi-stemmed tree *Corylus avellana* in a remnant temperate forest in central Iberian Peninsula from comparatively reduced liana infestation on *C. avellana* relative to co-occurring woody species.

Methods

Through principal component analysis and co-occurrence analysis, we studied the distribution and spatial association between woody species and the liana *H. helix*. We analyzed the relationship between the number of species in a plot and the number of species infested by the liana to test the hypothesis that *H. helix* is a generalist liana. Through generalized linear mixed models, we tested the dynamic-multi-stemmed growth form of *C. avellana* as a plausible life strategy to withstand, in the long run, the liana infestation. In particular, we tested (i) the relationship between stem size and the probability of *H. helix* infestation including all the tree species

within plots and (ii) the relationship between stem size and mortality as evidence of the stem turn over in the tree *C. avellana*.

Important Findings

Our results indicate that *H. helix* and *C. avellana* significantly co-occur in mature stands of this remnant temperate forest where pioneer woody species are absent. *Hedera helix* severely infests all the woody species whenever stem size exceed ≈ 25 cm perimeter and there is physical contact at the base of the stem. This implies that all the trees in the community are potential hosts for *H. helix*. Mixed models indicate that both, infestation by *H. helix* and stem mortality, are positively related to *C. avellana* stem perimeter. Reduced long-term infestation of the liana by means of a multi-stemmed growth form with high stem turnover in *C. avellana* might be an advantage with respect to unipodial tree species. Thus, the liana-tree coexistence pattern may be interpreted as an indirect positive interaction that, contrary to previous findings, results here in species dominance instead of species coexistence.

Keywords: indirect facilitation, species coexistence, species dominance, competition, liana infestation

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INTRODUCTION

Direct competitive interactions have a chief role driving species coexistence and dominant status in plant communities (Huston and De Angelis 1994; Tilman 1988). Particularly in size-structured communities such as forests, one-sided competition alone (e.g. competition for light) can explain forest

dynamics in the long-term (Kohyama and Takada 2009, 2012). In this regard, current forest models assume that taller trees pre-empt light resources of smaller trees; thus, tree growth and survival of understory species will demand different light yielding strategies and higher light use efficiency than overstory species (Onoda *et al.* 2014). Tree architecture and resource-use trade-offs are therefore of paramount importance

to explain mechanisms of tree species coexistence and competition (Kitajima and Poorter 2008; Poorter et al. 2012). In particular, adult tree stature is directly involved in the eventual dominance of tree species during secondary succession (Bose et al. 2014; Kunstler et al. 2016; Schamp and Aarssen 2009). However, in a riparian protected forest in the central Iberian Peninsula, dominant taller tree species such as *Populus nigra*, *Salix fragilis*, *Fraxinus angustifolia* or *Alnus glutinosa* are eventually replaced by the small tree *Corylus avellana* in mature forest stands. *Corylus avellana* is a small tree of 4–6 m tall with a multi-stemmed growth form that occupies an intermediate position between pioneer shrubs and late-successional trees. Interestingly, field observations indicate that the dominant status of *C. avellana* occurs only in the presence of the generalist liana *Hedera helix*. This observation suggests that dominance of *C. avellana* could be, at least in part, caused by direct competition between the liana and *C. avellana*'s competitors.

Lianas are a significant component of temperate and tropical forests, having a major contribution to aboveground biomass and biodiversity (Gentry 1991; Schnitzer and Bongers 2002). Lianas can induce mortality (Putz 1984; Putz and Mooney 1991), suppress regeneration (Schnitzer et al. 2000), and reduce growth and fecundity (Dillenburg et al. 1993; Gerwing 2001; Grauel and Putz 2004; Stevens 1987) of infested trees owing to mechanical damage, competition for light and interference for below-ground resources (van der Heijden and Phillips 2009; Schnitzer and Bongers 2002). Lianas are highly competitive species when adequate physical support allows them to reach the forest canopy (without investment in costly woody stems; Tobin et al. 2012). However, our knowledge of lianas as drivers of tree community structure and composition is still limited (Ingwell et al. 2010). One of the most studied aspects of lianas in tropical and temperate forests is the existence of preferences for specific hosts (Carrasco-Urra and Gianoli 2009; Ladwig and Meiners 2010; Leicht-Young et al. 2010; Muñoz et al. 2003). Hence, the co-occurrence of trees and lianas does not necessarily imply infestation and its ensuing negative consequences. Some lianas combine climbing with trailing growth forms that allow a fast spreading across the forest floor to seek for suitable host plants (Gianoli 2015; Isnard and Silk 2009). Accordingly, it has been hypothesized that lianas could play a key role via affecting tree interaction networks by differentially reducing the competitive ability of infested individuals, thus favouring non-infested ones (Pérez-Salicrup and Barker 2000; Pérez-Salicrup et al. 2001; Schnitzer and Carson 2010; Tobin et al. 2012). Although infestation preferences imply differential impacts on disparate tree species, little is known on how direct and indirect effects of lianas combine to affect the tree community composition and structure in the long-term. Indirect interactions are currently known to be decisive in shaping plant communities (Schöb et al. 2013). However, it is still poorly understood how multiple mechanistic pathways lead to species coexistence in space and time (Sotomayor and Lortie 2015).

In the present study, we document a case of indirect interactions, where coexistence between apparent antagonistic

species results from facilitative effects of the liana *H. helix* on the tree host *C. avellana* (Fig. 1). To document this interaction in a long-lasting community, we tested in mature forest stands of a temperate forest the following hypotheses: (i) there is significant spatial association between the liana *H. helix* and the target tree *C. avellana*, (ii) the liana is able to infest all the potential competitors of *C. avellana* (generalist behaviour) and (iii) only *C. avellana* can withstand a long-term liana infestation through a multi-stemmed growth form (e.g. high stem turnover that keeps stem size structure within minimum infestation probabilities). The latter hypothesis assumes that the infestation probability is size-dependent, i.e. that *H. helix* infestation is positively associated with tree host stem size (Castagneri et al. 2013). Experimental studies on indirect plant interactions suggest that indirect facilitation emerges when the negative consequences of direct competition between two species are exceeded by the benefits provided via suppression of a shared competitor (Levine 1999). Scaled to a multi-species context, these indirect pairwise interactions should influence species assembly and community structure by promoting species coexistence and thus community diversity (Aschehoug and Callaway 2015). Interestingly, and opposed to this multi-species experimental evidence (Aschehoug and Callaway 2015), the indirect facilitation expected in the study system should lead to species dominance because only one species is benefited from the negative effects of the generalist liana on the tree community. Support for this hypothesis could open new perspectives on the role of indirect interactions in structuring plant communities in terrestrial plant communities.

METHODS

Study area

The study area is located in the central-north Iberian Peninsula, within a remnant temperate forest growing at the margins of the Cega river (geographical coordinates: 41°21'34.5"N,

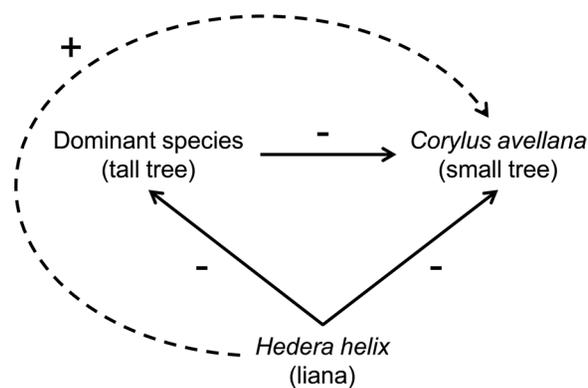


Figure 1: conceptual model to visualize the hypothesis of indirect facilitation of *C. avellana* by *H. helix* (adapted from Levine 1999). Solid lines represent the direct interactions and the dashed line represents the indirect interaction. Signs denote positive (+) or negative (-) interactions.

4°16'11.2"W; elevation: 799.8 m.a.s.l.; see map in online supplementary Fig. S1). The Cega valley is composed of clay and sandy materials that periodically collapse with strong floods (Guerra-Velasco *et al.* 2006). Although the area has a typical cool-Mediterranean climate with 12°C annual average temperature and 430 mm annual precipitation (Calonge 1987), microclimate conditions associated with valley topography have allowed the relict temperate vegetation to persist since the end of the late glacial period (Soriano *et al.* 2002). Strong flooding events, however, remove mature vegetation from the hillsides of the valley, setting the stage for the establishment of a rich pioneer successional community dominated by temperate shrubs such as *Lonicera xylosteum*, *Viburnum opulus*, *Crataegus monogyna*, *Rhamnus cathartica*, *Cornus sanguinea*, *Prunus spinosa*, *Rubus ulmifolius*, *Rubus caesius* and trees such as *Populus nigra*, *Frangula alnus*, *Fraxinus angustifolia* or *Alnus glutinosa* (Cuesta-Cano *et al.* 2007). The resulting pattern is a mosaic of vegetation patches with different degree of maturity that harbour more than 40 species of trees and shrubs.

The dominant liana: *H. helix*

Hedera helix is a well known liana species with a wide distribution in temperate habitats all over the world, either as a native or non-native taxon. This species is a very aggressive climbing plant as shown by the strong negative impacts exerted on the accompanying vegetation in natural (Yaman 2009) and invaded ecosystems (Metcalfe 2005). Along with the typical behaviour of root climbers, i.e. adhesive roots that firmly attach the liana to host trees, it includes trailing growth forms that enable the plant to rapidly spread across the forest floor seeking suitable host trees.

Field data and sampling design

We estimated the relative cover of all woody species as the orthogonal projection of individual crowns over the ground in 40 circular plots (20 m diameter) regularly distributed along a 10 km transect parallel to the river. Because crowns of different individuals can overlap, total percentage cover in a plot can exceed 100%. We laid out the sampling transect at the southern slope of the river as it is more homogeneous in terms of microclimatic conditions and topography, keeping a minimum distance of 10 m from the river to avoid periodical flooding influences.

We measured size (stem perimeter) of all stems larger than 5 cm perimeter that were in physical contact with the liana. Additionally, we visually estimated the forest canopy cover and recorded the percentage cover of *H. helix* in each plot. All the measurements and sampling were conducted at the end of the summer season (August–September) in 2012.

Sampling design and statistics

Species composition and dominance of the *Hedera*–*Corylus* association was first studied through ordination analysis (principal component analysis, PCA) using a covariance matrix based on the relative cover of each species. Ordination

analyses were conducted with CANOCO 4.5 (Lepš and Šmilauer 2003). Additionally, we analyzed pairwise co-occurrence patterns simultaneously for the complete pool of species in the community, by means of the pairwise approach described in Veech (2013, 2014). This analysis applies pure probability-based equations (Veech 2013) to identify the nature of the association for every pair of species in the community. The probabilistic model analytically determines (without data randomization) the probability that two species of a pair co-occur at an observed frequency different to that expected if the two species were distributed randomly with respect to each other. Associations of pairs of species are then identified as positive, negative or random based upon the values of observed frequencies relative to a pre-defined significance level of $P < 0.05$ (Veech 2013, 2014). We carried out this analysis using the R package 'co-occur' (Griffith *et al.* 2016).

To test for the particular positive spatial association between *H. helix* and *C. avellana*, we used a pairwise co-occurrence analysis with presence/absence data. We tested for association using the checkerboard unit (CU) index and a null distribution of CU obtained through randomization of presence/absence data. The pairwise co-occurrence index is computed as $(r_i - S)(r_j - S)$, where r_i and r_j are the total number of occurrences of species i and j , respectively, and S is the number of sites shared by both the i and j species (Stone and Roberts 1991). The null model was created from 10 000 permutations of data, maintaining that the occurrence of each species in the simulation was identical to the original data and that each sample was equally likely to be represented (i.e. fixed-equiprobable, Gotelli 2000). The standardized effect size (i.e. the number of standard deviations that the observed index is above or below the mean index of the simulated communities, Gotelli *et al.* 2002) is reported under the assumption that values below -2 represent co-occurrence. We used the software Ecosim 700 for co-occurrence analyses (Gotelli and Entsminger 1999).

We tested for liana host specificity by analysing the relationship between the number of woody species in a plot (potential hosts) and the number of woody species actually infested by the liana (realized hosts) using generalized linear models with Poisson distribution of residuals and log link function. The number of realized hosts in a plot should increase linearly with the number of potential hosts if the liana is a generalist climber. Because *H. helix* was never found to climb on shrub species with stems < 5 cm perimeter, even when they were contacted at the base of the stem (personal observations), we repeated the analysis including only tree species.

We studied the relationship between stem size and the probability of climbing using generalized linear mixed models (GLMM). Tree stem size has been previously shown to be relevant in liana–tree interactions (Carrasco-Urra and Gianoli 2009). Forest canopy cover and cover of *H. helix* were also included as variables potentially contributing to explain the probability of climbing since they affect the availability and quality of light and the contact with potential host stems, respectively. The response variable was a binomial variable with values 1

and 0 representing stems with and without lianas, respectively. For this analysis, we only considered those stems that were in physical contact with lianas at the base of stems, assuming that climbing is obviously not possible without contact with the liana. A total of 456 stems belonging to 168 woody plant individuals were identified and measured along the sampling transect. We fitted a logistic model with binomial distribution of error and a logit link function. The fitted equation is as follows:

$$p(\text{climbing} | X_i, \theta_i) = 1 / (1 + \exp^{-\left(\sum_i^n X_i \theta_i + \beta\right)})$$

where, $\sum_i^n X_i \theta_i + \beta$ represents the linear term including the set of i predictors (X) and associated parameters (θ) and the intercept parameter (β). We assumed dependency within stems belonging to the same individual. For this reason, we considered a random term with two components. On the one hand, we included dependency of individuals nested in plots affecting the probability of climbing (intercept in the model). On the other hand, we considered two potential hypotheses regarding differential climbing probabilities across potential host species: (i) probability of climbing differs across species (i.e. species affecting the intercept parameter of the model) or (ii) differences in the probability of climbing due to variability of stem perimeter is species-specific (i.e. species affecting the intercept parameter and the parameter associated with stem perimeter). We conducted the selection of the best random term using the Akaike information criterion corrected for small samples (AICc; Hurvich and Tsai 1993) following the rule that models exceeding in two units from the lowest AICc value will not be considered for inference (Burnham and Anderson 2002). After the selection of the best random term, we proceeded to test the validity of fixed factors (FC—forest canopy cover, HC—*Hedera* cover, SP—stem perimeter) on climbing probability. A null model including only the random term was also created to validate the supported fixed term. Fixed variables selection was conducted using a stepwise backward procedure on an initial full model including the three explanatory variables (FC, HC, SP). The selection of variables consisted on the elimination of each variable at a time to see how AICc varies compared with the AICc of the full model. When the elimination of a variable leads to an increment of at least four units of AICc then this variable was included in the final supported model; otherwise it was not included in the model.

To analyse the stem turnover in *C. avellana* we recorded whether stems were alive or dead in all the *C. avellana* individuals measured. With this information, and using a GLMM with binomial error distribution and a logit link function, we assessed the relationship between stem size and mortality (i.e. binomial variable, alive/dead). To this end, we compared a model including stem size as the predictor variable with a model including an intercept parameter as the only fixed term (e.g. no predictor variables). This comparison was conducted using the AICc.

RESULTS

Species composition and the *H. helix*-*C. avellana* association

The first axis of the PCA of species composition showed a pattern of segregation of *C. avellana* and *H. helix* from the other species (Fig. 2). This axis explained 39.6% of variance and reflected the high correlation between distribution of the liana and the tree throughout the forest. Co-occurrence analysis for *H. helix* and *C. avellana* using C -score supported this relationship, showing a significant spatial association of both species. Of the 40 circular plots, *C. avellana* occurred in 24 plots, *H. helix* in 27 plots and both species co-occurred in 22 plots. A total of 9998 simulated checkerboard units (thereafter CU) were lower than the observed CU and only 2 values were equal. The CU was 10.00 and the standardized size effect was -2.63044 . Hence, the probability for rejecting the null hypothesis of random distribution of species was $P = 0.0002$ (see Ecosim700 outputs in online supplementary Table 1).

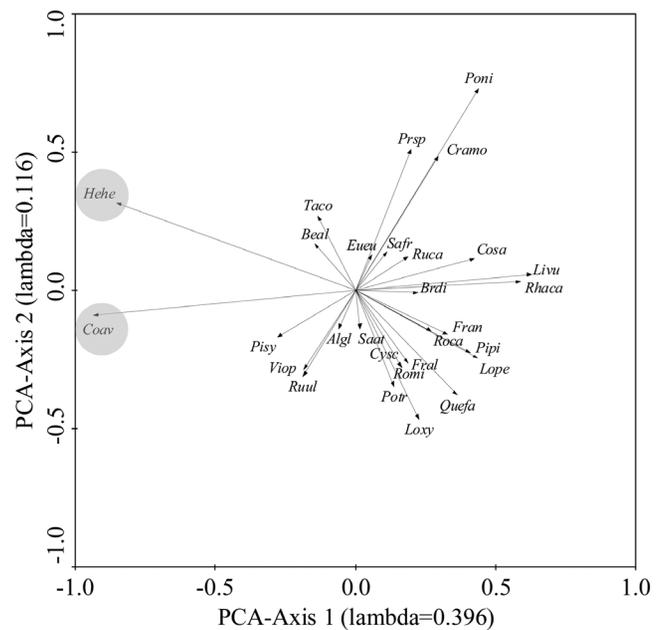


Figure 2: species distribution gradient (arrows) defined by 1st and 2nd principal components of PCA (species \times samples) in the bi-plot. The size and direction of arrows indicate strength and sign of correlation between species and principal components, respectively. The lambda parameter shows the proportion of total variance explained by a particular axis. Legend of species: Algl = *Alnus glutinosa*, Beal = *Betula alba*, Brdi = *Bryonia dioica*, Coav = *Corylus avellana*, Cosa = *Cornus sanguinea*, Cramo = *Crataegus monogyna*, Cysc = *Cytisus scoparius*, Eueu = *Euonymus europaeus*, Fral = *Frangula alnus*, Fran = *Fraxinus angustifolia*, Hehe = *Hedera helix*, Livu = *Ligustrum vulgare*, Lope = *Lonicera periclymenum*, Loxy = *Lonicera xylosteum*, Pipi = *Pinus pinaster*, Pisy = *Pinus sylvestris*, Poni = *Populus nigra*, Potr = *Populus tremula*, Prsp = *Prunus spinosa*, Quefa = *Quercus faginea*, Rhaca = *Rhamnus cathartica*, Romi = *Rosa micrantha*, Roca = *Rosa canina*, Ruca = *Rubus caesius*, Ruul = *Rubus ulmifolius*, Saat = *Salix atrocinerea*, Taco = *Tamus communis*, Viop = *Viburnum opulus*.

The pairwise analysis of co-occurrence for the whole community supported the significant association between *H. helix* and *C. avellana* (see online supplementary Fig. S2) and suggested a significant negative relationship between the liana and early successional shrub species such as *Ligustrum vulgare*, *Cornus sanguinea* or *Rhamnus cathartica*. The only shrub species that was positively associated with the liana was *Viburnum opulus* which is a Eurosiberian shrub species that inhabits the understory of mature forest stages.

Host specificity in *H. helix*

There was a significant and positive linear relationship between the number of potential hosts and the number of realized hosts ($R^2 = 0.27$, $F_{1,25} = 9.61$, $P = 0.004$; Fig. 3a and residual analyses in online supplementary Fig. S3). This relationship was stronger when shrubs were removed from the analysis ($R^2 = 0.84$, $F_{1,25} = 136.2$, $P < 0.001$; Fig. 3b) because none of the shrub species was infested by *H. helix*. In fact, only non-contacted trees or saplings <10 cm perimeter were free from *H. helix* infestation, which explains why in some plots the number of tree species with lianas was slightly lower than the total number of species.

Tree stem diameter and infestation by *H. helix*

We measured a total of 456 stems belonging to 168 woody plant individuals that were in contact with *H. helix*. Of the 456 stems measured, 148 (44.4%) of *C. avellana* and 89 of other species (72.3%) were actually climbed by lianas. Only 4 out of 45 individuals of *C. avellana* were not in physical contact with the liana at the base of the stems, so they were eventually discarded for this test. For the majority of the woody species measured, including *C. avellana*, the supported model suggested a ≈ 25 cm of stem perimeter threshold for climbing. For the species *Populus nigra*, the climbing threshold was slightly higher (i.e. ≈ 45 cm perimeter; Fig. 4). Neither FC nor HC were relevant factors to be included in the supported model (Table 1).

Stem turnover in *C. avellana*

A total of 48 out of 333 stems of *C. avellana* (14%) were dead at the time of field sampling. The backward selection of fixed effects pointed to stem perimeter (SP) as the only significant variable to be included in the model (Table 2). The best supported model (pseudo- $R^2_{\text{conditional}} = 0.69$) suggested that mortality is positively related to stem size. Thus, the probability of mortality is above 0.5 in stems above a 50 cm of perimeter and maximum mortality probability is reached in stems above 80 cm of perimeter (Fig. 5).

DISCUSSION

Corylus avellana and *H. helix* are co-dominant plant species in this remnant temperate forest as shown by their spatial association and the scarcity of accompanying tree species. Moreover, their significant segregation from pioneer shrubs

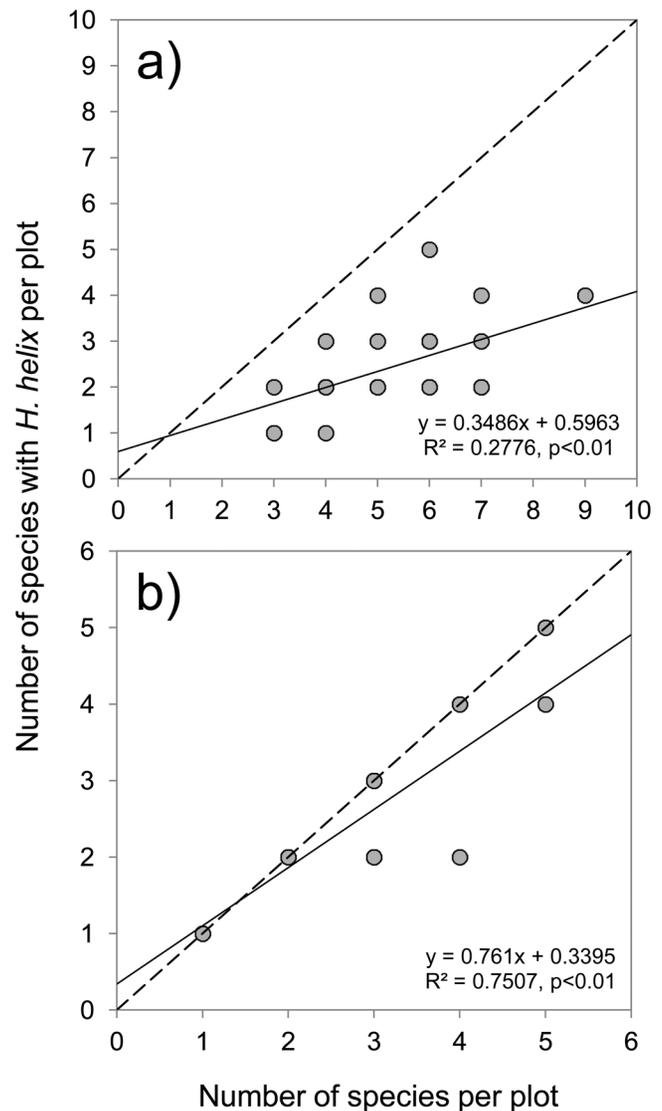


Figure 3: linear regression analysis for (a) number of woody species per plot that were infested by *H. helix* vs. number of woody species per plot, and (b) number of tree species per plot infested by *H. helix* vs. number of tree species per plot. Dashed lines represent regression lines with slope 1.

such as *Rhamnus cathartica*, *Cornus sanguinea* or *Ligustrum vulgare*, indicates the late-successional character of this association. As tree species regenerate, a shaded habitat excludes most of the pioneer shrub species from the understory, thus providing a suitable habitat for the liana. Schnitzler (1995), Küppers *et al.* (1996) and Laskurain *et al.* (2004) reported the mid to late-successional occurrence of *H. helix* in temperate forests, even though seedling emergence of *H. helix* can occur in almost every soil type (Laskurain *et al.* 2004) and light environment (Bauer and Thöni 1988; Hoflacher and Bauer 1982). Contrary to pioneer shrubs, *C. avellana* and a few shade-tolerant shrub species such as *Viburnum opulus* and *Lonicera xylosteum*, remain in the forest understory despite of the shaded

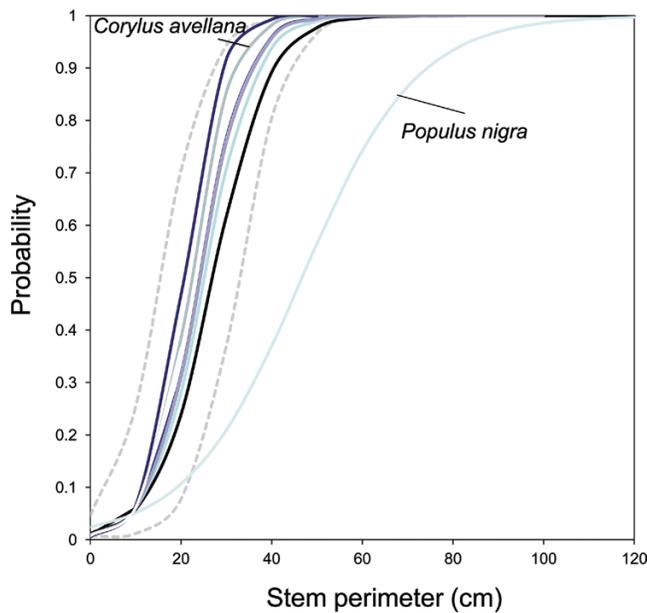


Figure 4: climbing probability expressed as a function of stem perimeter with their respective 95% confidence intervals (grey dashed lines). Models are based on the variance associated with the random structure ‘individuals nested within plots’ plus residual variance. Coloured lines represent species-specific relationships between stem size and climbing probability for the 12 species recorded in sampled plots (*Alnus glutinosa*, *Corylus avellana*, *Crataegus monogyna*, *Frangula alnus*, *Fraxinus angustifolia*, *Ligustrum vulgare*, *Lonicera xylosteum*, *Populus nigra*, *Rhamnus cathartica*, *Salix atrocinerea*, *Salix fragilis* and *Viburnum opulus*).

Table 1: selection of random and fixed (backward selection) terms using the Akaike information criterion corrected for small sample sizes (AICc) to explain the climbing probability of *H. helix*

Models	AICc	ΔAICc
Random term		
(1 Plot/Ind) + (SP Species)	435.03	0
(1 Plot/Ind) + (1 Species)	439.13	4.1
(1 Plot/Ind)	440.68	5.65
Fixed term (backward selection)		
FC + HC + SP	435.03	0
FC	434.19	-0.84
HC	433.42	-1.61
SP	450.79	15.76
Intercept only	448.12	13.09

Plot/Ind denotes individuals nested within plots. Abbreviations: FC = forest canopy cover (i.e. orthogonal projection on the ground); HC = *H. helix* cover; Ind = individuals; Plot = sampling plots; SP = stem perimeter (cm). Selected terms are highlighted in bold.

conditions imposed by taller trees. Eventually, *H. helix* can preclude seedling emergence (Metcalf 2005) through mechanisms such as allelopathy (Bonanomi et al. 2006) which is in

Table 2: selection of random and fixed (backward selection) terms using the Akaike information criterion corrected for small sample sizes (AICc) to explain stem mortality probability (*C. avellana*)

Models	AICc	ΔAICc
Fixed term (backward selection)		
FC + SP	200.30	0
FC	210.41	10.11
SP	199.55	-1.75
Intercept only	209.16	8.86

Abbreviations: FC = forest canopy cover (i.e. orthogonal projection on the ground); SP = Stem perimeter (cm). Selected terms are highlighted in bold letters.

accordance with the fact that mature stages of the forest are composed only of adult *C. avellana* and *H. helix*, and a few/ scattered adult tree individuals of species such as *P. nigra*, *F. angustifolia* or *A. glutinosa*. Kull and Niinemets (1993) have demonstrated that *C. avellana* is a shade-tolerant tree species that inhabits the understory of deciduous temperate forests (Herbst et al. 2008). However, deep shading from tall trees can negatively affect its growth and performance (Bennett 1986). At a biogeographical scale, palynological records suggest that the expansion of *C. avellana* throughout Central Europe during the early Holocene required recurrent disturbance events that reduced competition from tall temperate tree species (Finsinger et al. 2006; Tinner and Lotter 2001). Downscaled to a contemporary temperate forest, the liana *H. helix* could act as a regular disturbance agent reducing the competitive ability of taller trees thus indirectly favouring understory species.

The generalist feature of *H. helix* is critical to understand the aforementioned top-down influence of the liana on the tree community. *H. helix*, in agreement with our second hypothesis, can infest all the tree species in the forest whenever it contacts the base of tree stems. Although we did not measure the effects of *H. helix* infestation on tree hosts, strong negative effects have long been reported in this and other liana species (Ingwell et al. 2010; Schnitzer and Bongers 2002). For example, changes in wood anatomical characteristics and reduced growth rates have been observed in black alder trees infested by *H. helix* in a floodplain forest in Turkey (Yaman 2009). At a community level, lianas are known to accelerate gap dynamics in temperate and tropical forest by predisposing large/ infested trees to be windthrown or collapse during extreme flooding events. In invaded ecosystems, the ‘ivy desert’ concept has emerged to denote a limited number of canopy trees together with an absence of understory and ground cover plants after long-term colonization by *H. helix* (Westbrook 1998). Hence, any mechanism able to hinder liana infestation would indirectly enable a species to be more competitive within the community.

According to our third hypothesis, results suggest that stems with a perimeter size above 20–25 cm increase *H. helix* infestation beyond a 0.5 probability. Similar patterns of

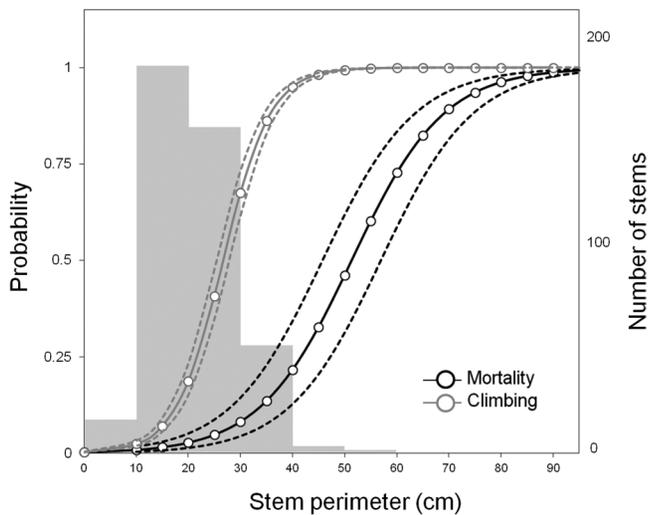


Figure 5: probability of (i) climbing by *H. helix* (grey solid line) and (ii) stem mortality (black solid line) as a function of stem size (perimeter at breast height) in *C. avellana*. Dashed lines represent 95% confidence intervals based on summed residual variance and the variance associated with random factors. Grey bars in the background represent stem frequency distribution along perimeter classes: <10 cm, 10–19.9 cm, 20–29.9 cm, 30–39.9 cm, and ≥ 40 cm.

H. helix infestation have been observed in an alluvial forest of NW Italy (Castagneri *et al.* 2013), where most trees in the study plots carried the liana and tree size was a primary factor explaining *H. helix* infestation. Other authors found stem diameter to be an important tree feature influencing liana infestation in tropical forests (DeWalt *et al.* 2000; Nabe-Nielsen 2001). Carrasco-Urra and Gianoli (2009) observed a significant positive relationship between trunk diameter and the relative abundance of adhesive climbers in a temperate forest in southern Chile. In agreement, neither shrub species nor tree saplings are infested by *H. helix* in our studied forest (personal observation). In turn, *C. avellana* was the tree species less affected by *H. helix* infestation despite the liana was often in contact with the base of the stems. On the one hand, mean stem size in *C. avellana* was lower than the climbing probability threshold (≈ 20 cm perimeter). On the other hand, our model showed that a 0.5 probability of stem mortality in *C. avellana* is reached at a 50 cm perimeter. Thus, keeping mean stem size below the infestation probability threshold reduces the likelihood of a long-term infestation in *C. avellana* relative to other tree species.

We cannot completely rule out the possibility that factors such as shared habitat preferences or successional dynamics may contribute to the pattern observed. Indeed, such a pattern could result from a number of different mechanisms of species interactions (see Levine 1999). It is important to note, however, that cases of indirect facilitation in forest communities have seldom been reported. This might be due to dominance of direct negative effects over indirect positive effects (Pagès and Michalet 2003) and/or prevalence of indirect

negative interactions in complex interaction networks (Xiao and Michalet 2013). Although our sampling was designed to locate sampling units in a homogeneous environment, certain microhabitat preferences shared by *H. helix* and *C. avellana* might have contributed to the spatial association detected. Moreover, if these specific microhabitat preferences are not shared with other tree or shrub species, then this liana-tree association would be possible even if indirect positive effects were weak. Alternatively, it could be conceived that co-occurrence of *H. helix* and *C. avellana* might be—at least partly—associated with differential abilities of species to thrive under strong flooding events, which are common in the study system. Prolonged flooding might have a comparatively stronger impact on big trees. In this regard, Ernst and Brooks (2003) reported that prolonged flooding events favour shrubby vegetation over tall tree species. However, prolonged flooding events negatively affect *H. helix* as a consequence of increased soil anoxia (Schnitzler and Heuzé 2006). Therefore, the *Coryllus–Hedera* association might benefit from flooding to some extent, as long as flooding does not prolong in time as to compromise *H. helix*.

A number of empirical studies and modelling approaches have highlighted the role of indirect facilitation in promoting species coexistence (Vandermeer *et al.* 1985; Stone and Roberts 1991; Levine 1999; Pennings and Callaway 1996; Callaway and Pennings 2000; but see also Michalet 2003; Sotomayor and Lortie 2015). In the present study, observational data concerning composition, interaction and co-occurrence patterns suggest that competition of *H. helix* with co-occurring tree species can lead to indirect facilitation of the small tree *C. avellana*. Our results, however, do not support previously reported findings that indirect interactions promote species coexistence. For example, Callaway and Pennings (2000) found that indirect facilitation in coastal salt marsh communities significantly alter the cover and density of dominant and rare plant species. Furthermore, Beltrán *et al.* (2012) have revealed the crucial role of indirect interactions for the coexistence of congeneric plant species. Ecosystem invasibility, a community property related to non-native species establishment, has also been suggested to be enhanced by indirect facilitation via competitive suppression (Madrigal *et al.* 2011; Madrigal-González *et al.* 2013). Recently, experimental evidence provided by Aschehoug and Callaway (2015) showed how strong indirect interactions can maintain diversity even in the absence of functional differentiation within coexisting species. All the above-mentioned studies illustrate the role of indirect facilitation enhancing species coexistence and diversity. In contrast, our study suggests that indirect facilitation by an antagonist species might lead to co-dominance instead of coexistence when one of the interacting species, the liana in this case, act as a biotic filter that excludes most species. We are aware that our study is based on correlational evidence, mainly because of the difficulty of experimental manipulations in long-lived species. Nonetheless, it provides a new perspective to study dominant associations in forest ecosystems, which have been seldom explained by indirect

facilitation derived from direct competition in the community. Furthermore, these observations may contribute to improve our knowledge of the mechanisms through which lianas shape community structure in forest ecosystems.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Journal of Plant Ecology* online.

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