School of Biology

Assessing spatial autocorrelation in biodiversity data in the Western Swiss Alps

First step project of Master in Science in Behaviour, Evolution & Conservation

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ABSTRACT

Aim Spatial autocorrelation is frequent in ecological data because the properties of nearby locations are more similar than expected by chance. The impact of this phenomenon on species distribution models is controversial: some argues that it has an important impact on model parameters, whereas others claim that it does not necessary induces bias. In this study, we investigated the extent of spatial autocorrelation in biodiversity data to provide an assessment of this phenomenon.

Location The Western Swiss Alps.

Methods The following groups of species were studied during this project: *Bombus*, *Lepidoptera*, *Orthoptera*, *Vegetation*, *Forest* and *Fungi.* Spatial autocorrelation was investigated in species composition with Mantel correlograms. For each species, environmental variables and spatial distribution models residuals, spatial autocorrelation was assessed using Moran's *I* correlograms.

Results Species composition in the different groups displays low spatial autocorrelation. Most of the species under investigation shows moderate positive spatial autocorrelation in the first distance classes, which becomes negative in the last distance classes. Climatic predictors display more spatial autocorrelation than topographic variables. In the residuals of species distribution models, almost no species show spatial autocorrelation.

Main conclusions This study highlighted that spatial autocorrelation is only low to moderate in the different groups of species and the environmental data under study. More importantly, residuals were not autocorrelated, meaning that species distribution models are not biased by spatial autocorrelation.

Keywords Spatial autocorrelation, Moran's *I*, Mantel, correlogram, *Lepidoptera*, *Orthoptera*, *Bombus*, *Fungi*, vegetation, species distribution models, Western Swiss Alps

INTRODUCTION

The geographical distribution of a species is one of the most central information in ecology. It is determined by biotic, abiotic and historical processes which operate at different spatial and temporal scales (Guisan & Thuiller, 2005). Understanding how these processes are shaping species distribution patterns is of interest for both ecological and biogeographical research (Guisan & Thuiller, 2005). Modeling habitat of species is a key to understand the patterns of biodiversity (Williams & Hero, 2001) and the species requirements (Corsi *et al.*, 1999; Jarvis & Robertson, 1999).

Species distribution models (SDMs) are increasingly important tools for number of applications, such as conservation planning or estimating the potential distribution of species under various future scenarios, like climate change or habitat fragmentation (Franklin, 2010; Peterson, 2011). SDMs are empirical models relating the occurrence or the abundance of species found in a known location to a set of environmental variables characterizing those locations (Guisan & Zimmermann, 2000). When constructing an SDM, several sources of uncertainty associated with data and methods can be introduced into the model (Beale & Lennon, 2012). Among them, spatial autocorrelation is a recurrent reported concern (Cablk *et al.*, 2002; Segurado *et al.*, 2006; Dormann, 2007).

Spatial autocorrelation is frequently found in ecological data because nearby locations tend to be more similar in species occurrences and/or physical characteristics than expected by chance (Legendre, 1993). A variable is considered to be spatially autocorrelated when it is possible to predict its value at some spatial points from the known values at other sampling points, whose locations in space are also determined (Legendre & Fortin, 1989). Spatial autocorrelation is induced either by endogenous or exogenous processes (Legendre & Legendre, 1998). In the endogenous case, the spatial pattern is a result of contagious biotic processes within the variable itself such as growth, reproduction, migration and mortality (Legendre, 1993). It is known as “true spatial autocorrelation” (Legendre *et al.*, 2002) or “inherent spatial autocorrelation” (Fortin & Dale, 2005). Spatial autocorrelation generated by exogenous processes independent of the variable itself is referred as “induced spatial dependence” (Fortin & Dale, 2005) or “spatial dependency” (Legendre *et al.*, 2002). In this case, spatially structured environmental factors such

as geomorphological processes or climate constraints are likely to cause spatial structures in the species distribution (Legendre et al., 2002; Diniz-Filho et al., 2003).

Spatial autocorrelation could be seen both as a source of information about spatial pattern, structure and processes and a methodological issue (Gould, 1970). An autocorrelated observation is less informative than an independent observation meaning that a new sample point is not carrying one complete degree of freedom (Cliff & Ord, 1981). This lack of independence among observations (Legendre & Fortin, 1989) is therefore problematic for classical statistical tests. In regression models used for species distribution analysis, it will bias downwards the variance leading to incorrect tests of the significance of the expected value. Thus, spatial autocorrelation might have an impact on model parameters and model building and fit (Dormann, 2007). Such impact on parameters had been highlighted in several studies (Mauricio Bini et al., 2009; Hodges & Reich, 2010), notably showing that it can invert the sign of the relationship between the parameter and the response variable (Kühn, 2007). However, other studies claim that spatial autocorrelation does not necessarily induce bias (Diniz-Filho *et al.*, 2003) and that it has a relatively small effect on predictions accuracy compared to other issues (Thibaud *et al.*, 2014).

In this study, we aimed at investigating the extent of spatial autocorrelation on the biodiversity data in the Western Swiss Alps to determine its potential impact. This will provide the first large-scale assessment of this phenomenon in the study area using species as well as environmental data and spatial correlograms. For that purpose, we first evaluated spatial autocorrelation in different ensembles of species (fungi, insects and plants) and then in each species. As recommended by Lichstein *et al.* (2002), an examination of the correlograms of environmental variables was also conducted. Finally, residuals of distribution models of orthopteran and lepidopteran species were tested for spatial autocorrelation.

According to a previous study (Garcillán & Ezcurra, 2003), we expect that spatial autocorrelation over the complete study area should be of low amplitude, mainly because of the heterogeneity of the landscape.

MATERIAL AND METHODS

Study area

The study area is located in the western Swiss Alps (Vaud, Switzerland, 46°10'–46°30' N; 6°60'–7°10' E) and is covering approximately 700 km^2. The region is formed by alpine meadows, glaciers and agricultural lands. A large elevation gradient is present, ranging from 375 to 3210 m and the climate is temperate with annual temperature and precipitation varying from 8°C and 1200 mm at 600 m to -5°C and 2600 mm at 3000 m (Bouët, 1985). A detailed description of the study area is provided by Randin *et al* (2006).

Data

Vegetation data

912 vegetation plots of 4 m^2 were selected following a random-stratified sampling design (Hirzel & Guisan, 2002) and the presence-absence of each species was recorded in each plot (Dubuis *et al.*, 2011). Only vascular species in open and non-woody vegetation were sampled. This resulted in a dataset composed by 795 species.

Forest data

A grid of 400 m over all of the study area was used; therefore, a point was recorded every 400 m (Hartmann *et al.*, 2009). If a point was falling into a forest, a field sampling was made. The field sampling was done in a circle with center at the coordinates of the point and with a radius of 10 m. All vascular plant species were recorded. The final dataset consisted of 667 species.

Insect data

Insect species were sampled in 50 m x 50 m plots selected with a balanced stratified random sampling design (Hirzel & Guisan, 2002) and centered on the coordinates of previous 4 m^2 vegetation sampling sites

93 (Dubuis *et al.*, 2011). 202 sites were investigated for bumblebees and orthopteran species (Pradervand *et*
94 *al.*, 2012; Pradervand *et al.*, 2014) and 192 for lepidopteran species (Pellissier *et al.*, 2013). 28 species of
95 bumblebees, 190 species of *Lepidoptera* and 41 species of *Orthoptera* were identified. The sampling was
96 performed during the insects' active hours (10:00 to 17:00) under good weather conditions (i.e., little wind,
97 sunny, and temperatures above 15°C). Presence-absence of species was first recorded in four sub-squares
98 of 10 m by 10 m located at the four cardinal points of the large square and subsequently in the complete 50
99 m square.

100 *Fungi data*

101 94 plots of 25 m^2 in non-forested areas were selected following a random-stratified sampling strategy
102 (Hirzel & Guisan, 2002). Five soil cores of 10 cm^3 per plot were sampled from the top 10 cm of the soil after
103 removing plant litter surface. Community composition was determined by DNA extraction from 250 mg dry
104 soil for each sample followed by PCR and pyrosequencing. The processing and computation of the raw
105 reads leads to the definition of 3339 ITS2 OTUs. Pellissier *et al*. (2014) give a detailed description of the
106 data collection, sequencing and bioinformatic analyses done.

107 *Environmental data*

108 The description of the environmental variables used for the analysis is provided in Table 1. The variables
109 number of degree days (*ddeg*), moisture index (*mind*), number of frost days (*sfroyy*), slope (*slp*), global solar
110 radiation (*srad*) and topography (*topo*) were retrieved from the WSL database with 25 m resolution for the
111 *Vegetation, Forest* and *Fungi* groups and with 50 m for the *Bombus*, *Lepidoptera* and *Orthoptera* groups.
112 The summer temperature (*sumtemp*) was calculated as the mean temperature of the months of July,
113 August and September at a 50 m resolution. The variable distance to forest (*dist_forest*) was defined as the
114 Euclidean distance to the nearest forest at a 50 m resolution. The normalized digital vegetation index
115 (*NDVI*) uses reflectance of the canopy in the red (R) and near-infrared (NIR) and was calculated at a 10 m
116 resolution according to the following formula:

$$NDVI = (NIR - R)/(NIR + R)$$

A complete description of the methods used to obtain the soil properties such as pH, total nitrogen (*N*) and phosphorus (*P*) content is provided by Dubuis *et al.* (2013).

Assessing spatial autocorrelation

Species communities

Whole-community spatial autocorrelation was investigated in the following datasets: *Vegetation*, *Forest*, *Lepidoptera*, *Orthoptera*, *Bombus* and *Fungi*. A matrix of ecological distances was compared to a geographical distances matrix based on Euclidean distances between plots by means of a Mantel test (Mantel, 1967) using the VEGAN package (Oksanen *et al.*, 2007) in R (R Development Core Team, 2014). For presence/absence data, the matrix of ecological distances between all pairs of sites was built for each group using the distance corresponding to Sørensen's coefficient (1948). For abundance data, the distance corresponding to Bray-Curtis coefficient (1957) was used, which is the quantitative equivalent of Sørensen's. They are defined respectively as

$$D_S(x_i, x_j) = 1 - \frac{2a}{2a + b + c}$$

$$D_{BC}(x_i, x_j) = 1 - \frac{2W}{A + B}$$

where $D_S(x_1, x_2)$ and $D_{BC}(x_1, x_2)$ are respectively the Sørensen's and Bray-Curtis dissimilarity between plot *i* and plot *j*, *a* is the number of species present in both plot *i* and *j*, *b* is the number of species present in quadrat *i* but not in *j*, *c* is the number of species present in plot *j* but nor in *i*, *W* is the sum of the minimum abundances of the various species, *A* is the total number of specimens present in site *i* and *B* is the number of specimens present in site *j*. To investigate the patterns and significance of spatial autocorrelation across the study area, Mantel correlograms were constructed. Data were divided into distance classes and for each one of them, a Mantel rank correlation coefficient (r_m) was calculated. Significance of spatial autocorrelation in each distance classes was tested using 1000 permutations. Correlograms were considered as globally significant only when at least one of the Mantel correlation coefficient was

significant at the Bonferonni corrected level (Oden, 1984; Legendre & Legendre, 1998). Within each correlogram, p-values for each distance class were corrected for multiple comparisons using Holm's correction (Holm, 1979).

The Jaccard coefficient was used as well and analysis were also run using NCF library. The Mantel correlograms were similar regardless of the technique employed.

Species and environmental predictors

Only species with more than 30 occurrences throughout all sampled plots were retained for the analysis, as recommended by Legendre and Fortin (1989). Accordingly, 208 plants in the vegetation dataset, 309 plants in the forest dataset, 52 Fungi, 10 Orthoptera, 51 Lepidoptera and 14 Bombus species were tested for spatial autocorrelation. For environmental predictors, an assessment of spatial autocorrelation in variables used to calibrate species distribution models in the different groups was done in the plots where each group was respectively sampled. Moran's *I* values and correlograms were calculated for each species and each environmental predictors using the NCF package (Bjørnstad, 2009) in R (R Development Core Team, 2014) and significance was assessed using 1000 permutations. The Moran index estimates an autocorrelation coefficient that varies between −1.0 (negative autocorrelation) and 1.0 (positive autocorrelation), with values near zero indicating no spatial autocorrelation. The calculation is done by comparing geographic neighbors in terms of their deviation from the mean of all observations. An increment of 2500 m was used for each distance classes, which is a compromise between resolution of the correlogram (better resolution with narrower classes) and power of the test (test more powerful when there are more pairs in a distance class). Correlograms were considered as globally significant only when at least one of the Moran's *I* value was significant at the Bonferonni corrected level (Oden, 1984; Legendre & Legendre, 1998). Within each correlogram, the significance of Moran's I for each distance class was tested using Holm's correction for multiple comparisons (Holm, 1979).

Model residuals

Species distribution models were performed for lepidopteran and orthopteran species (D'Amen, In prep.). The models were calibrated using a set of bioclimatic and landscape explanatory variables: the annual sum of radiation (in kJ $m^{-2}year^{-1}$), the mean yearly number of frost days, the mean NDVI, the distance to forest (in m), the mean temperature (°C) during the months of July, August and September and the degree-days above zero values. Single-species models were performed with BIOMOD2 package (Thuiller *et al.*, 2009) in R (R Development Core Team, 2014) using a generalized linear model (GLM) and a generalized additive model (GAM). Tests for spatial autocorrelation in the mean of residuals of both species distribution models were performed for lepidopteran and orthopteran species with more than 30 occurrences using the same method used for species autocorrelation.

RESULTS

Spatial autocorrelation in species communities

Bombus, *Lepidoptera* and *Orthoptera* follow the same pattern of spatial autocorrelation: positive spatial autocorrelation occurs in the first distance classes, followed by random oscillations around zero and finally, negative autocorrelation in the last distance lags (Fig. 1A, 1B, 1C). For *Vegetation* and *Forest,* positive spatial autocorrelation occurs until 1500 m and 1250 m respectively, followed by negative spatial autocorrelation (Fig. 1D, 1E). Significant positive spatial autocorrelation is present only until 2500 m for *Fungi* (Fig. 1F). In all groups, the amplitude of spatial autocorrelation was low (ranging from -0.04 to 0.15).

Spatial autocorrelation in each species

In the *Bombus* group, most of the species does not display spatial autocorrelation (Fig. 2A); only five species out of 14 shows significant spatial autocorrelation (Fig. S1). For the *Lepidoptera* group, 38 out of 51 species exhibit spatial autocorrelation (Fig. S2). The pattern is similar for most of the species: spatial autocorrelation is positive in the first distance classes and becomes negative for the last distance classes (Fig. 2B). All species of the *Orthoptera* group display spatial autocorrelation (Fig. S3), which is positive in the first distance lags, fluctuates for the intermediary lags and becomes negative for the final classes (Fig. 2C). 201 out of the 208 species of the *Vegetation* group exhibit spatial autocorrelation (Fig. S4). The pattern is the same for most of the species: positive spatial autocorrelation in the first distance classes, which gets negative in the latter distance classes (Fig. 2D). For the *Forest* group, all species display spatial autocorrelation (Fig. S5) and the pattern is similar as for the *Vegetation* group (Fig. 2E). In the *Fungi* group, 7 OTUs out of 51 show spatial autocorrelation (Fig. S6), but positive or negative significant spatial autocorrelation is distributed randomly across the distance classes (Fig. 2F).

Spatial autocorrelation in environmental variables

Environmental variables used for *Bombus*, *Lepidoptera* and *Orthoptera* all display spatial autocorrelation. The variables temperature degree days (*ddeg;* Fig. 3A), number of frost day (*sfroyy*; Fig. 3B), summer temperature (*sumtemp*; Fig. 3D), normalized digital vegetation index (*NDVI*; Fig. 3E) and distance to forest (*dist_forest;* Fig. 3F) exhibit the same pattern: positive spatial autocorrelation until 10 km approximately, which becomes negative in the last distance classes with fluctuation for the intermediate classes. The variable global solar radiation (*srad*) displays positive spatial autocorrelation in the first distance class and then only random fluctuation (Fig. 3C).

For the *Vegetation* and *Forest* groups, the variable temperature degree days (*ddeg*; Fig. 4A) and moisture index (*mind*; Fig. 4B) present the same pattern as described in the *Bombus*, *Lepidoptera* and *Orthoptera* groups. Autocorrelation for global solar radiation (*srad*) is significant in all distance classes, but always very close to 0 (Fig. 4C). For the topographical predictors slope (*slp;* Fig. 4D) and topography (*topo*; Fig. 4E), spatial autocorrelation is fluctuating around the zero line and is significant only for some distance classes.

In the *Fungi* group, the variables temperature degree days with a zero threshold (*ddeg0*; Fig. 5A) and moisture index (*mind*; Fig. 5B) exhibit the same pattern of spatial autocorrelation: positive for the first two distance classes and then fluctuating between negative and positive values of Moran's *I*. The variables *pH* (Fig. 5C) and nitrogen (*N;* Fig. 5D) does not show significant spatial autocorrelation. The variable phosphorus (*P*; Fig. 5E) displays negative spatial autocorrelation for the second distance class; for all other classes, spatial autocorrelation is not significant.

Spatial autocorrelation in models residuals

Spatial autocorrelation is found in the model residuals of 6 out of 51 species of the *Lepidoptera* group (Fig. S7). In the *Orthoptera* group, only the model residuals of one species out of 10 display spatial autocorrelation (Fig. 6B). Positive spatial autocorrelation occurs in the first and sixth distance classes and negative spatial autocorrelation in the seventh class (Fig. S8).

DISCUSSION

Spatial autocorrelation in communities, species and environment

As expected, a low degree of spatial autocorrelation was found in all groups and in the majority of species. In ecology, datasets are virtually always spatially autocorrelated regardless of the species under consideration (Malanson, 1985; McGeoch & Price, 2004; Tognelli & Kelt, 2004; Dormann, 2007; Santos *et al.*, 2012). In this study, values of spatial autocorrelation were low, especially for species composition.

A decrease in species similarity with distance is common in ecology (Bell, 2001). This phenomenon is led by different mechanisms such as decreasing similarity in environmental properties (Nekola & White, 1999), limited dispersal of organisms (Hubbell, 2001) as well as spatial arrangement and landscape characteristics (Garcillán & Ezcurra, 2003). A rapid decrease in species similarity was previously highlighted in heterogeneous landscapes with important dispersal barriers (Garcillán & Ezcurra, 2003). Hence, the heterogeneous nature of our study area might explain the low spatial autocorrelation found in species composition.

Several methods have been recommended to take into account spatial autocorrelation. These include *a priori* procedures such as sampling design with sufficient space between plots (Guisan & Theurillat, 2000) or *a posteriori* methods such as correction of the number of degree of freedom (Legendre, 2002) and incorporating an autocovariate term in the model (Lichstein *et al.*, 2002). Random or systematic sampling designs as performed for this study are advocated to prevent spatial autocorrelation among observations (Legendre & Fortin, 1989) and might be the reason why spatial autocorrelation was only low to moderate in the study area.

Alternately, the spatial scale used for this study might have an impact on the pattern highlighted. Spatial autocorrelation varies according to the resolution under consideration and is expected to be more noticeable at smaller spatial scales (Collingham *et al.*, 2000). This is particularly true if endogeneous factors generate spatial autocorrelation, since most of these causes occur at small spatial scale (e.g. less than 1 km) and are rare at larger scales (Guisan & Thuiller, 2005; Dormann, 2007). In this study, spatial autocorrelation

was assessed at a large scale (e.g. distance lags of 2.5 km). So small-scale spatial autocorrelation might have not been highlighted, explaining the low values of spatial autocorrelation observed.

The current amount of studies is not enough to make generalization about where spatial autocorrelation will be strong or weak, but it is known that strong environmental trends will increase the strength of spatial autocorrelation caused by exogenous factors (Lodge *et al.*, 2007). In our study, environmental variables are not showing a strong spatial structure, and as it was previously reported by Segurado *et al.* (2006), topographical descriptors are less spatially autocorrelated than climatic predictors. It is difficult to distinguish between endogenous or exogenous causes of spatial autocorrelation (Diniz-Filho *et al.*, 2003), but we can presume that most of the spatial autocorrelation that was highlighted in this study is of exogenous origin. Exogenous factors such as soil composition or climate displaying spatial autocorrelation can drive species occurrences to be more similar than expected by chance in neighboring sites (Dormann, 2007). Including them in the statistical model may lower or even eliminate spatial autocorrelation in the species distribution model residuals (Higgins *et al.*, 1999; Fisher *et al.*, 2002).

Spatial autocorrelation in residuals

Several authors underline the need to test for spatial autocorrelation in the residuals of species distribution models (Dormann, 2007; Kühn, 2007; Kissling & Carl, 2008). Different processes such as unmeasured structured environmental variables or population dynamics could drive the presence of spatial autocorrelation in the model residuals (Dray *et al.*, 2012). In the case of spatially autocorrelated residuals, some advocate the use of spatial models, which incorporate an autocovariate term (Lichstein *et al.*, 2002; Dormann, 2007). Nevertheless, the use of spatial models is quiet controversial. A major concern is that models with an autocovariate term are not transferable in space, because each site will have a different landscape structure (Guisan & Thuiller, 2005; Segurado *et al.*, 2006). Moreover, it remains unknown in which circumstances spatial models provide better estimates of parameters compared to non-spatial models (Kissling & Carl, 2008).

In our study, no spatial autocorrelation was found in the residuals for the majority of orthopteran and lepidopteran species. If no spatial autocorrelation is found in the residuals, this suggests that the

model is not bias statistically (Diniz-Filho *et al.*, 2003). Nevertheless, models are not strict tests of causality and bias in model parameters may still be a potential problem, because of factors such as confounding correlation (Levin, 1992). These problems are not linked to spatial autocorrelation, but to the regression technique itself (Diniz-Filho *et al.*, 2003).

Conclusion and perspectives

Although investigation of spatial autocorrelation should become a routine procedure when performing multiple regression models (Diniz-Filho *et al.*, 2003), it should not be systematically considered as a nuisance (Legendre, 1993). Spatial autocorrelation can be seen as an opportunity in various ways; it can provide a description of the spatial structure (Legendre & Fortin, 1989; Mistral *et al.*, 2000), assess the impact of positional uncertainty (Naimi *et al.*, 2011) or determine if variation in species abundances is driven by neutral processes such as dispersal (Diniz-Filho *et al.*, 2012).

This study suggests that spatial autocorrelation is not a major concern in biodiversity data in the Western Swiss Alps. This perspective is in agreement with a previous study which highlighted that spatial autocorrelation has only a small effect on the model parameters compared to other uncertainty factors such as a missing covariate or the sample size (Thibaud *et al.*, 2014).

Spatial autocorrelation was almost inexistent in the residuals of the species distribution models of lepidopteran and orthopteran species. For further studies, an assessment of spatial autocorrelation in the residuals of other groups of species would probably provide stronger support for the low impact of this phenomenon. Furthermore, global spatial autocorrelation was assessed for this study. To provide a better understanding of the ecological processes in place, additional studies on local spatial autocorrelation (Ord & Getis, 2001) could be of interest to provide a better insight in this ecological paradigm (Legendre, 1993).

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BIBLIOGRAPHY

Beale, C.M. & Lennon, J.J. (2012) Incorporating uncertainty in predictive species distribution modelling. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 247-258.

Bell, G. (2001) Neutral macroecology. *Science*, **293**, 2413-2418.

Bjørnstad, O.N. (2009) *ncf: spatial nonparametric covariance functions. R package version 1.1-3*. Available online at http://cran.r-project.org/web/packages/ncf/.

Bouët, M. (1985) *Climat et météorologie de la Suisse romande*. Payot, Lausanne.

Bray, J.R. & Curtis, J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological monographs*, **27**, 325-349.

Cablk, M., White, D. & Kiester, A.R. (2002) Assessment of spatial autocorrelation in empirical models in ecology. *Predicting species occurrences: issues of scale and accuracy. Island Press, Washington DC*, pp. 429-440.

Cliff, A.D. & Ord, J.K. (1981) *Spatial Processes: Models & Applications*. Pion, London.

Collingham, Y.C., Wadsworth, R.A., Huntley, B. & Hulme, P.E. (2000) Predicting the Spatial Distribution of Non-Indigenous Riparian Weeds: Issues of Spatial Scale and Extent. *Journal of Applied Ecology*, 13-27.

Corsi, F., Duprè, E. & Boitani, L. (1999) A large-scale model of wolf distribution in Italy for conservation planning. *Conservation Biology*, **13**, 150-159.

Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global ecology and Biogeography*, **12**, 53-64.

Diniz-Filho, J.A.F., Siqueira, T., Padial, A.A., Rangel, T.F., Landeiro, V.L. & Bini, L.M. (2012) Spatial autocorrelation analysis allows disentangling the balance between neutral and niche processes in metacommunities. *Oikos*, **121**, 201-210.

317 Dormann, C.F. (2007) Effects of incorporating spatial autocorrelation into the analysis of species
318 distribution data. *Global Ecology and Biogeography*, **16**, 129-138.

319 Dray, S., Pelissier, R., Couteron, P., Fortin, M.J., Legendre, P., Peres-Neto, P.R., Bellier, E., Bivand, R.,
320 Blanchet, F.G., De Caceres, M., Dufour, A.B., Heegaard, E., Jombart, T., Munoz, F., Oksanen, J.,
321 Thioulouse, J. & Wagner, H.H. (2012) Community ecology in the age of multivariate multiscale
322 spatial analysis. *Ecological Monographs*, **82**, 257-275.

323 Dubuis, A., Pottier, J., Rion, V., Pellissier, L., Theurillat, J.P. & Guisan, A. (2011) Predicting spatial patterns of
324 plant species richness: a comparison of direct macroecological and species stacking modelling
325 approaches. *Diversity and Distributions*, **17**, 1122-1131.

326 Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Vittoz, P. & Guisan, A. (2013) Improving the prediction
327 of plant species distribution and community composition by adding edaphic to topo-climatic
328 variables. *Journal of Vegetation Science*, **24**, 593-606.

329 Fisher, R.N., Suarez, A.V. & Case, T.J. (2002) Spatial patterns in the abundance of the coastal horned lizard.
330 *Conservation Biology*, **16**, 205-215.

331 Fortin, M.-J. & Dale, M.R.T. (2005) *Spatial analysis: a guide for ecologists*. Cambridge University Press.

332 Franklin, J. (2010) *Mapping species distributions: spatial inference and prediction*. Cambridge University
333 Press.

334 Garcillán, P.P. & Ezcurra, E. (2003) Biogeographic regions and β-diversity of woody dryland legumes in the
335 Baja California peninsula. *Journal of Vegetation Science*, **14**, 859-868.

336 Gould, P. (1970) Is Statistix Inferens the geographical name for a wild goose? *Economic geography*, 439-
337 448.

338 Guisan, A. & Theurillat, J.-P. (2000) Equilibrium modeling of alpine plant distribution: how far can we go?
339 *Phytocoenologia*, **30**, 353-384.

340 Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological*
341 *modelling*, **135**, 147-186.

342 Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models.
343 *Ecology letters*, **8**, 993-1009.

344 Hartmann, P., Fouvy, P. & Horisberger, D. (2009) L'Observatoire de l'écosystème forestier du canton de
345 Vaud: espace de recherche appliquée| The Forest Ecosystem Observatory in Canton Vaud: a field of
346 applied research. *Schweizerische Zeitschrift für Forstwesen*, **160**, s2-s6.

347 Higgins, S.I., Richardson, D.M., Cowling, R.M. & Trinder-Smith, T.H. (1999) Predicting the landscape-scale
348 distribution of alien plants and their threat to plant diversity. *Conservation Biology*, **13**, 303-313.

349 Hirzel, A. & Guisan, A. (2002) Which is the optimal sampling strategy for habitat suitability modelling.
350 *Ecological modelling*, **157**, 331-341.

351 Hodges, J.S. & Reich, B.J. (2010) Adding spatially-correlated errors can mess up the fixed effect you love.
352 *The American Statistician*, **64**, 325-334.

353 Holm, S. (1979) A simple sequentially rejective multiple test procedure. *Scandinavian journal of statistics*,
354 65-70.

355 Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography (MPB-32)*. Princeton
356 University Press.

357 Jarvis, A.M. & Robertson, A. (1999) Predicting population sizes and priority conservation areas for 10
358 endemic Namibian bird species. *Biological Conservation*, **88**, 121-131.

359 Kissling, W.D. & Carl, G. (2008) Spatial autocorrelation and the selection of simultaneous autoregressive
360 models. *Global Ecology and Biogeography*, **17**, 59-71.

361 Kühn, I. (2007) Incorporating spatial autocorrelation may invert observed patterns. *Diversity and*
362 *Distributions*, **13**, 66-69.

363 Legendre, P. (1993) Spatial autocorrelation: Trouble or new paradigm? *Ecology*, **74**, 1659-1673.

364 Legendre, P. & Fortin, M.J. (1989) Spatial pattern and ecological analysis. *Vegetatio*, **80**, 107-138.

365 Legendre, P. & Legendre, L. (1998) *Numerical Ecology, Second english edition*. Elsevier.

366 Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M. & Myers, D. (2002) The consequences of
367 spatial structure for the design and analysis of ecological field surveys. *Ecography*, **25**, 601-615.

368 Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943-1967.

369 Lichstein, J.W., Simons, T.R., Shriner, S.A. & Franzreb, K.E. (2002) Spatial autocorrelation and autoregressive
370 models in ecology. *Ecological monographs*, **72**, 445-463.

371 Lodge, L., Rachael, H.E., Anderson, B.J., de Groot, A., Bill, A., McQueen, A.A.M., Steel, J.B., Mistral, M.,
372 Mason, N.W.H. & Bastow Wilson, J. (2007) Spatial autocorrelation in plant communities: vegetation
373 texture versus species composition. *Ecography*, **30**, 801-811.

374 Malanson, G.P. (1985) Spatial autocorrelation and distributions of plant species on environmental
375 gradients. *Oikos*, 278-280.

376 Mantel, N. (1967) The detection of disease clustering and a generalized regression approach. *Cancer*
377 *research*, **27**, 209-220.

378 Mauricio Bini, L., Diniz-Filho, J.A.F., Rangel, T.F., Akre, T.S.B., Albaladejo, R.G., Albuquerque, F.S., Aparicio,
379 A., Araujo, M.B., Baselga, A. & Beck, J. (2009) Coefficient shifts in geographical ecology: an empirical
380 evaluation of spatial and non-spatial regression. *Ecography*, **32**, 193-204.

381 McGeoch, M.A. & Price, P.W. (2004) Spatial abundance structures in an assemblage of gall-forming
382 sawflies. *Journal of Animal Ecology*, **73**, 506-516.

383 Mistral, M., Buck, O., Meier-Behrmann, D.C., Burnett, D.A., Barnfield, T.E., Scott, A.J., Anderson, B.J. &
384 Wilson, J.B. (2000) Direct measurement of spatial autocorrelation at the community level in four
385 plant communities. *Journal of Vegetation Science*, **11**, 911-916.

386 Naimi, B., Skidmore, A.K., Groen, T.A. & Hamm, N.A.S. (2011) Spatial autocorrelation in predictors reduces
387 the impact of positional uncertainty in occurrence data on species distribution modelling. *Journal of*
388 *Biogeography*, **38**, 1497-1509.

389 Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of*
390 *Biogeography*, **26**, 867-878.

391 Oden, N.L. (1984) Assessing the significance of a spatial correlogram. *Geographical Analysis*, **16**, 1-16.

392 Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J. & Suggests, M. (2007) The
393 vegan package. *Community ecology package*,

394 Ord, J.K. & Getis, A. (2001) Testing for local spatial autocorrelation in the presence of global
395 autocorrelation. *Journal of Regional Science*, **41**, 411-432.

396 Pellissier, L., Alvarez, N., Espíndola, A., Pottier, J., Dubuis, A., Pradervand, J.N. & Guisan, A. (2013)
397 Phylogenetic alpha and beta diversities of butterfly communities correlate with climate in the
398 western Swiss Alps. *Ecography*, **36**, 541-550.

399 Pellissier, L., Niculita-Hirzel, H., Dubuis, A., Pagni, M., Guex, N., Ndiribe, C., Salamin, N., Xenarios, I., Goudet,
400 J., Sanders, I.R. & Guisan, A. (2014) Soil fungal communities of grasslands are environmentally
401 structured at a regional scale in the Alps. *Molecular Ecology*, **23**, 4274-4290.

402 Peterson, A.T. (2011) *Ecological niches and geographic distributions (MPB-49)*. Princeton University Press.

403 Pradervand, J.-N., Pellissier, L., Randin, C.F. & Guisan, A. (2014) Functional homogenization of bumblebee
404 communities in alpine landscapes under projected climate change. *Climate Change Responses*, **1**, 1-
405 10.

406 Pradervand, J.-N., Dubuis, A., Reymond, A., Sonnay, V., Gelin, A. & Guisan, A. (2012) Quels facteurs
407 influencent la richesse en orthoptères des Préalpes vaudoises? *Bulletin de la Société Vaudoise des*
408 *Sciences Naturelles*, **93**, 155-173.

409 R Development Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation
410 for Statistical Computing, Vienna. Available at: http://www.r-project.org.

411 Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based
412 species distribution models transferable in space? *Journal of Biogeography*, **33**, 1689-1703.

413 Santos, S., Aarts, G., Luttikhuizen, P.C., Campos, J., Piersma, T. & van der Veer, H.W. (2012) Site-specific
414 distribution of the bivalve Scrobicularia plana along the European coast. *Marine Ecology Progress*
415 *Series*, **471**, 123-134.

Segurado, P., Araújo, M.B. & Kunin, W.E. (2006) Consequences of spatial autocorrelation for niche-based models. *Journal of Applied Ecology*, **43**, 433-444.

Sørensen, T. (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter*, **5**, 1-34.

Thibaud, E., Petitpierre, B., Broennimann, O., Davison, A.C. & Guisan, A. (2014) Measuring the relative effect of factors affecting species distribution model predictions. *Methods in Ecology and Evolution*, **5**, 947-955.

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD–a platform for ensemble forecasting of species distributions. *Ecography*, **32**, 369-373.

Tognelli, M.F. & Kelt, D.A. (2004) Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. *Ecography*, **27**, 427-436.

Williams, S.E. & Hero, J.-M. (2001) Multiple determinants of Australian tropical frog biodiversity. *Biological Conservation*, **98**, 1-10.

TABLES

Table 1 Descriptions of the environmental variables for which spatial autocorrelation was investigated. Groups of species for which a variable is relevant are mentioned, as well as references to previous studies using those variables as predictors of the species distribution.

Variables	Abbreviations	Units	Descriptions	Groups of species	References
Temperature degree days	ddeg	°C day year^{-1}	Sum of days multiply by temperature > 3°C or 0°C (for *Fungi*)	Vegetation, Forest, Lepidoptera, Orthoptera, Fungi	Pellissier *et al.* (2014), Pradervand *et al.* (2012), Dubuis *et al.* (2011)
Moisture index	mind	mm day^{-1}	Amount of precipitation minus the potential evapotranspiration (average of monthly values June-August)	Vegetation, Forest, Fungi	Pellissier *et al.* (2014), Dubuis *et al.* (2011)
Soil pH	pH	unitless	Measure of acidity or basicity	Fungi	Pellissier (2014)
Nitrogen	N	mg/g of soil	Total nitrogen content	Fungi	Pellissier (2014)
Phosphorus	P	mg/g of soil	Total phosphorus content	Fungi	Pellissier (2014)
Frost days	sfroyy	day	Annual average number of frost days during	Lepidoptera,	Pradervand *et al.* (2012)

			the growing season	Orthoptera	
Global solar radiation	srad	kJ m^{-2} day^{-1}	Monthly average of daily global solar radiation	Vegetation, Forest, Lepidoptera, Orthoptera	Pradervand *et al.* (2012; 2014), Dubuis *et al.* (2011)
Summer temperature	sumtemp	degrees celsius	Mean temperature during the months of July, August and September	Lepidoptera, Orthoptera	D'Amen (pers. comm.)
Normalized Digital Vegetation Index	NDVI	unitless	Index of plant photosynthetic activity	Lepidoptera, Orthoptera	D'Amen (pers. comm.)
Distance to forest	dist_forest	meters	Euclidean distance from the closest forest	Lepidoptera, Orthoptera	D'Amen (pers. comm.)
Slope	slp	degrees	Slope inclination	Vegetation, Forest	Dubuis *et al.* (2011)
Topography	topo	unitless	Topographic position	Vegetation, Forest	Dubuis *et al.* (2011)

FIGURES

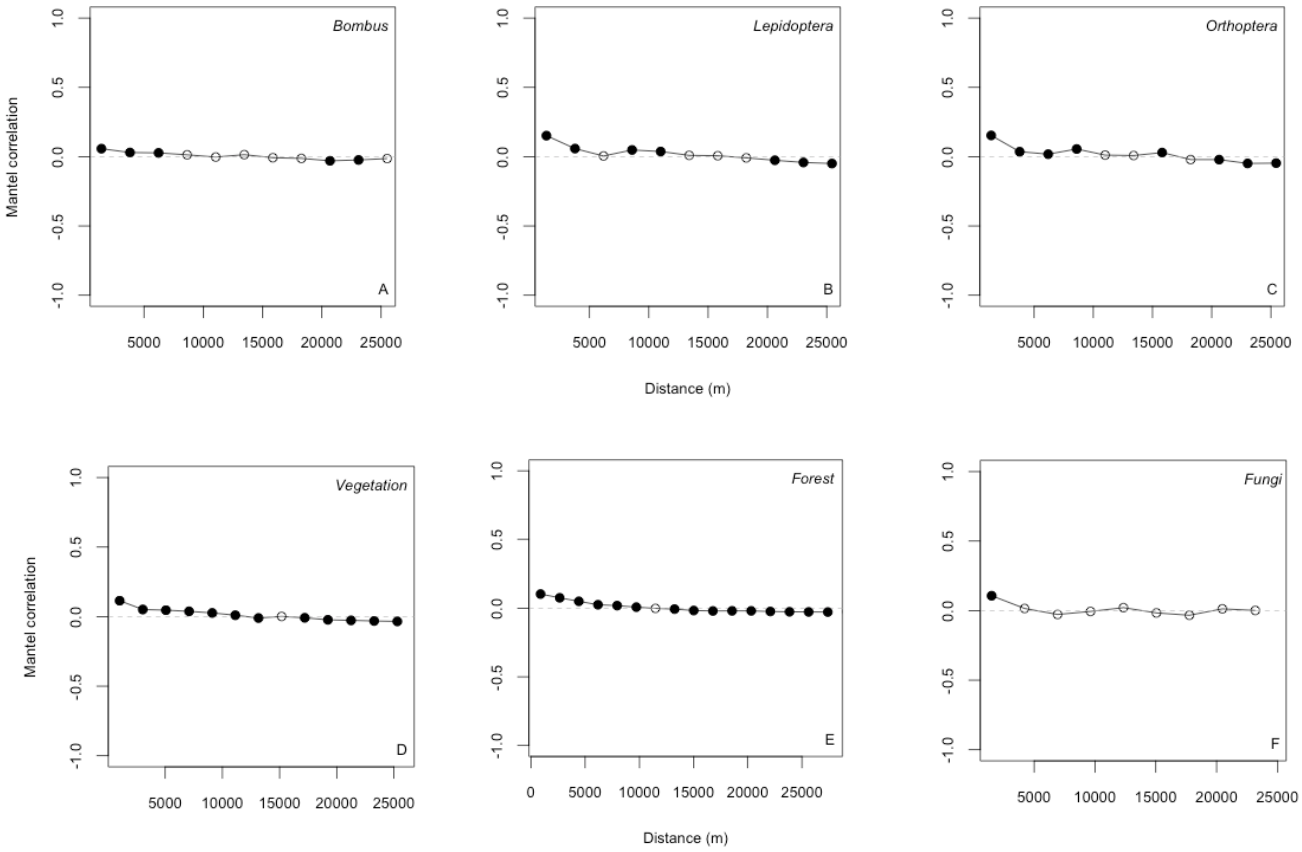
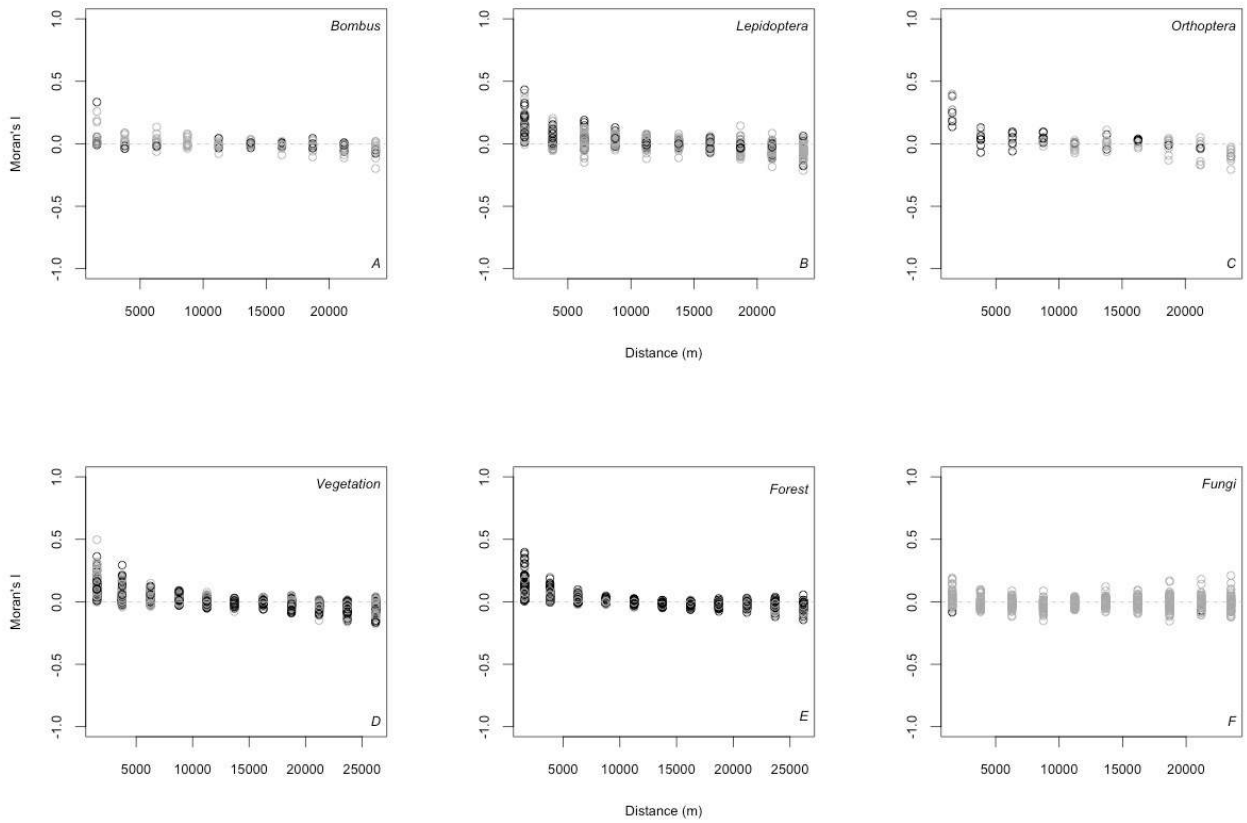
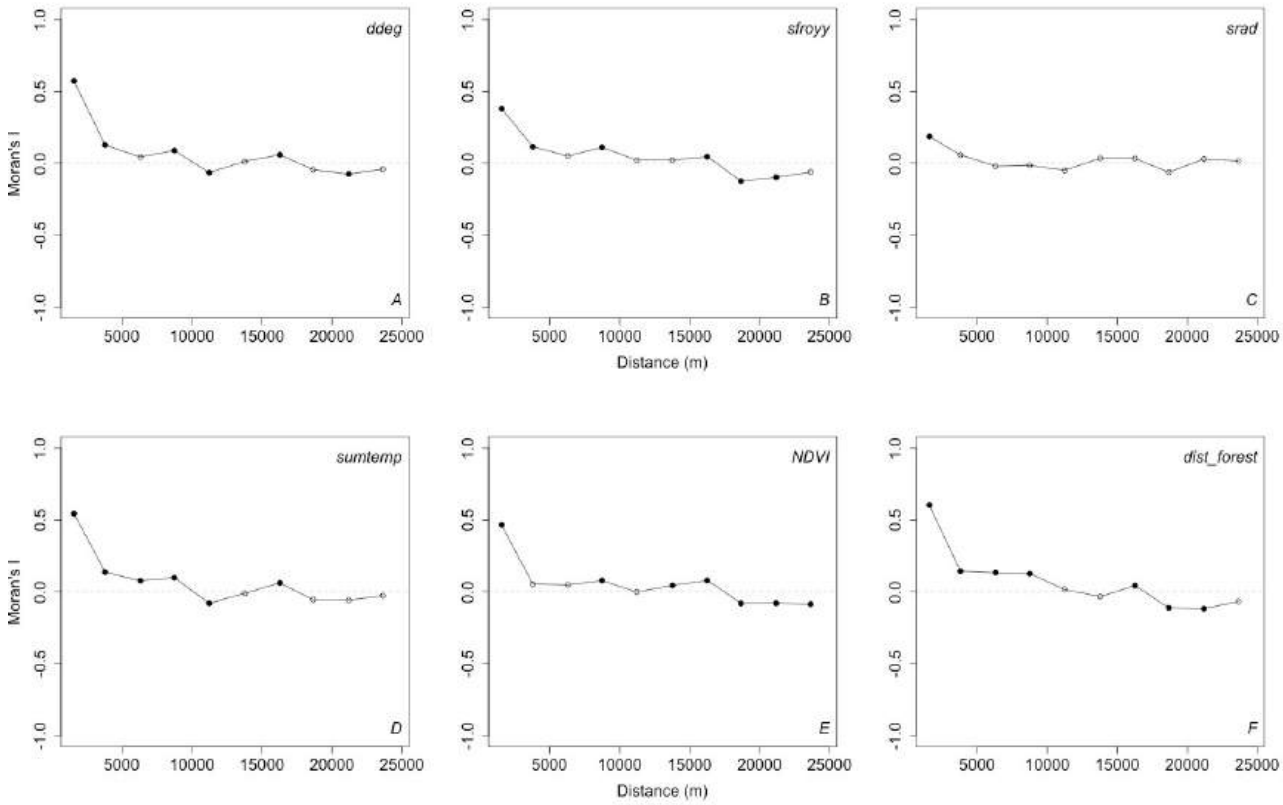


Figure 1 Spatial autocorrelation of species composition based on Mantel correlograms for the following groups of species: *Bombus*, *Lepidoptera*, *Orthoptera*, *Vegetation*, *Forest* and *Fungi*. All correlograms are globally significant at the α = 0.05 level since several individual values are significant after Bonferroni correction. Filled symbols are significant values after Holm's correction for multiple testing (α=0.05). Distances up to 2/3 of the maximum distance between two observations are represented.



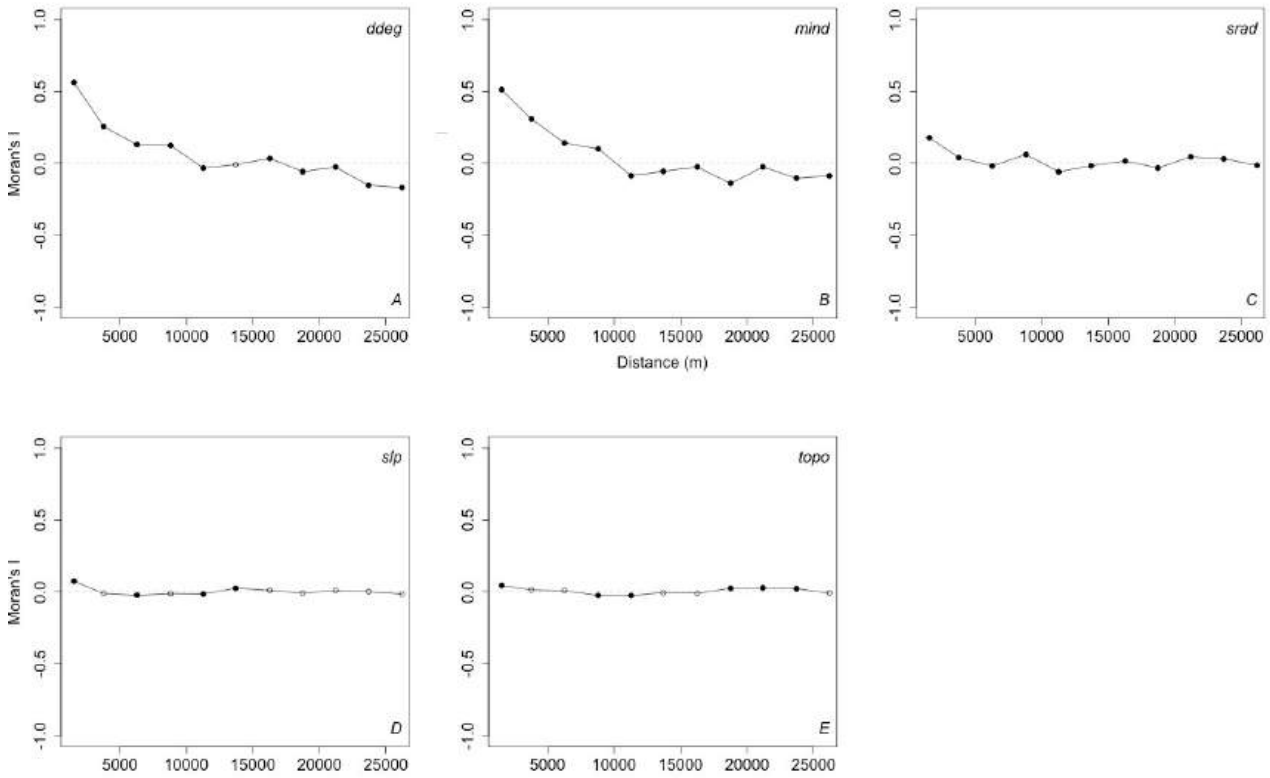
441

442 **Figure 2** Spatial autocorrelation of each individual species based on Moran's I correlograms. For each
443 distance class, a point represents a species. Black circles are significant values after Holm's correction for
444 multiple testing (α=0.05). Distances up to 2/3 of the maximum distance between two observations are
445 represented. Separate spatial correlograms per species are available in the supplementary material (Fig. S1-
446 S6).



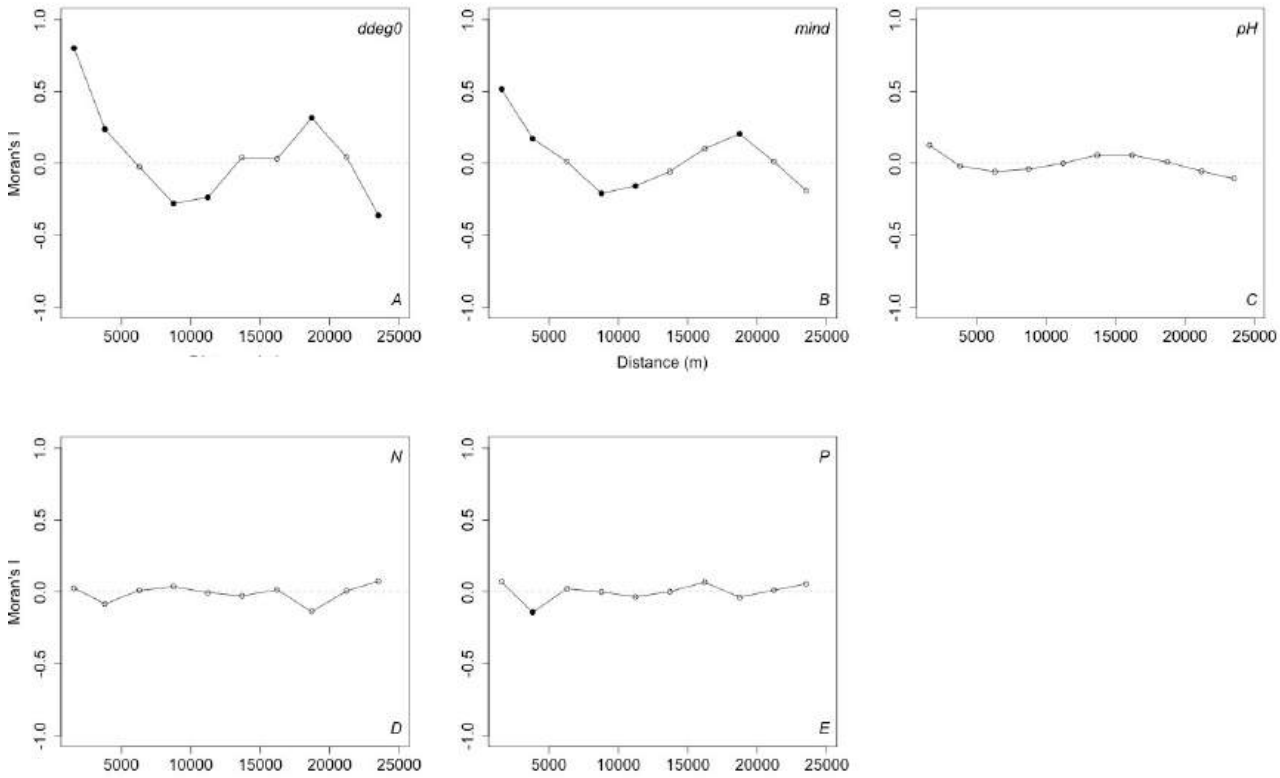
447

448 **Figure 3** Spatial autocorrelation of environmental variables used to predict the distribution of species of the
449 *Bombus*, *Lepidoptera* and *Orthoptera* groups based on Moran's *I* spatial correlograms. Spatial
450 autocorrelation of temperature degree days (*ddeg*), number of frost days (*sfroyy*), global solar radiation
451 (*srad*), summer temperature (*sumtemp*), normalized digital vegetation index (*NDVI*) and distance to forest
452 (*dist_forest*) are showed. All correlograms are globally significant at the α = 0.05 level since several
453 individual values are significant after Bonferroni correction. Filled symbols are significant values after
454 Holm's correction for multiple testing (α=0.05). Distances up to 2/3 of the maximum distance between two
455 observations are represented.



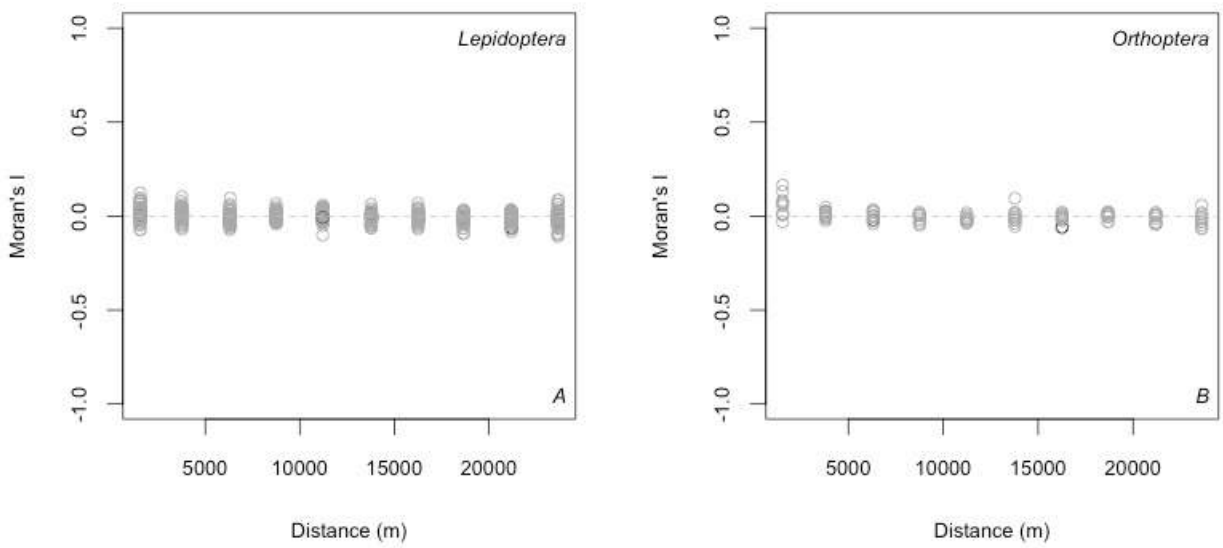
456

457 **Figure 4** Spatial autocorrelation of environmental variables used to predict the distribution of species of the
458 *Vegetation and Forest* groups based on Moran's *I* spatial correlograms. Spatial autocorrelation of
459 temperature degree days (*ddeg*), moisture index (*mind*), global solar radiation (*srad*), slope (*slp*) and
460 topography (*topo*) are showed. All correlograms are globally significant at the $\alpha = 0.05$ level since several
461 individual values are significant after Bonferroni correction. Filled symbols are significant values after
462 Holm's correction for multiple testing ($\alpha=0.05$). Distances up to 2/3 of the maximum distance between two
463 observations are represented.



464

465 **Figure 5** Spatial autocorrelation of environmental variables used to predict the distribution of *Fungi* based
466 on Moran's *I* spatial correlograms. Spatial autocorrelation of tempererature degree days with a zero
467 threshold (*ddeg0*), moisture index (*mind*), *pH*, nitrogen (*N*) and phosphorus (*P*) are showed. Filled symbols
468 are significant values after Holm's correction for multiple testing (α=0.05). Correlograms with at least one
469 significant value were all globally significant at the α = 0.05 level since several individual values are
470 significant after Bonferroni correction. Distances up to 2/3 of the maximum distance between two
471 observations are represented.



472

473 **Figure 6** Spatial autocorrelation of the residuals of the distribution model for each species from the
474 *Lepidoptera* and *Orthoptera* groups based on Moran's I correlograms. For each distance class, a point
475 represents a species. Black circles are significant values after Holm's correction for multiple testing
476 (α=0.05). Distances up to 2/3 of the maximum distance between two observations are represented.
477 Separate spatial correlograms per species are available in the supplementary material (Fig. S7-S8).

SUPPORTING INFORMATION

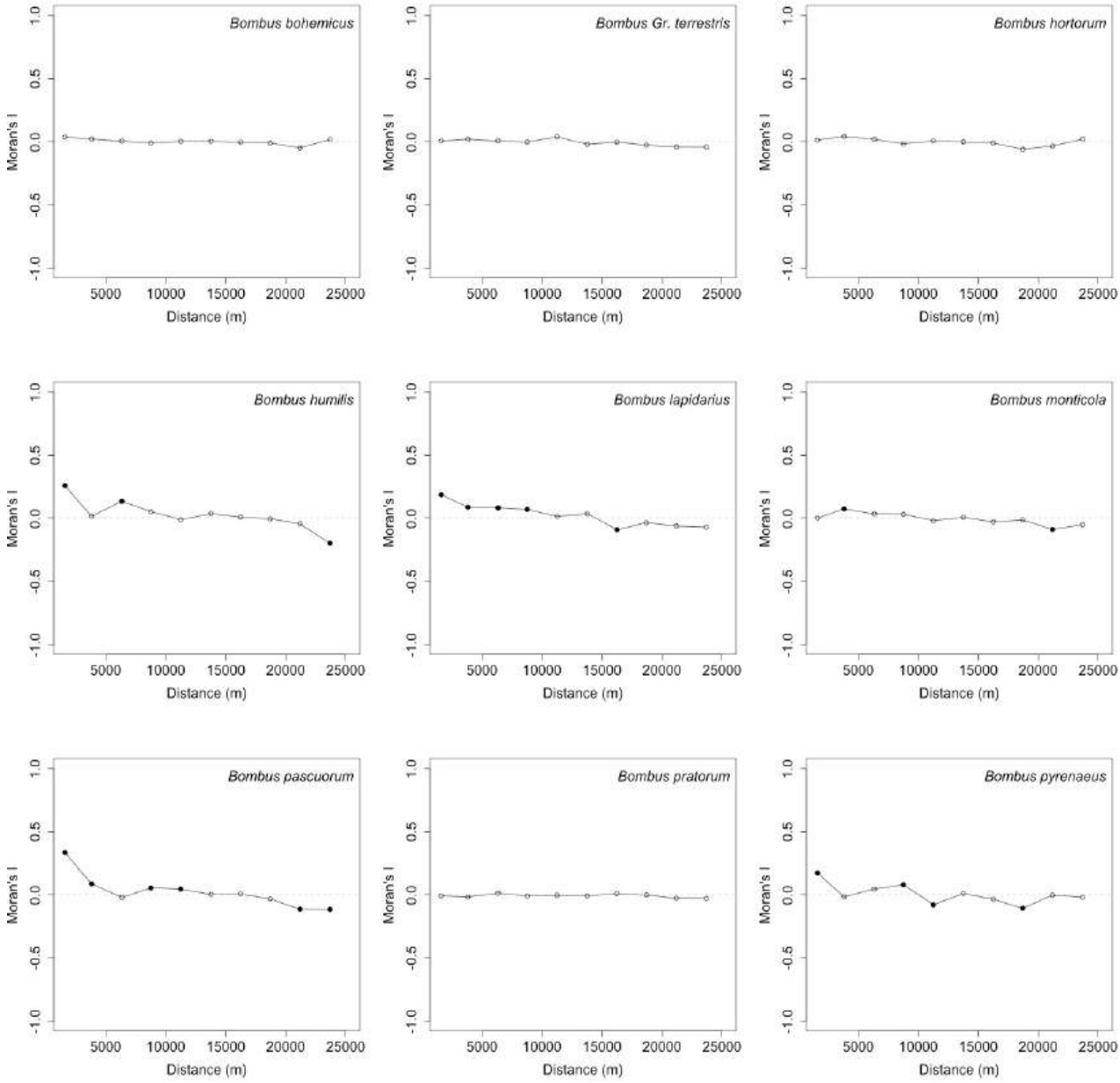
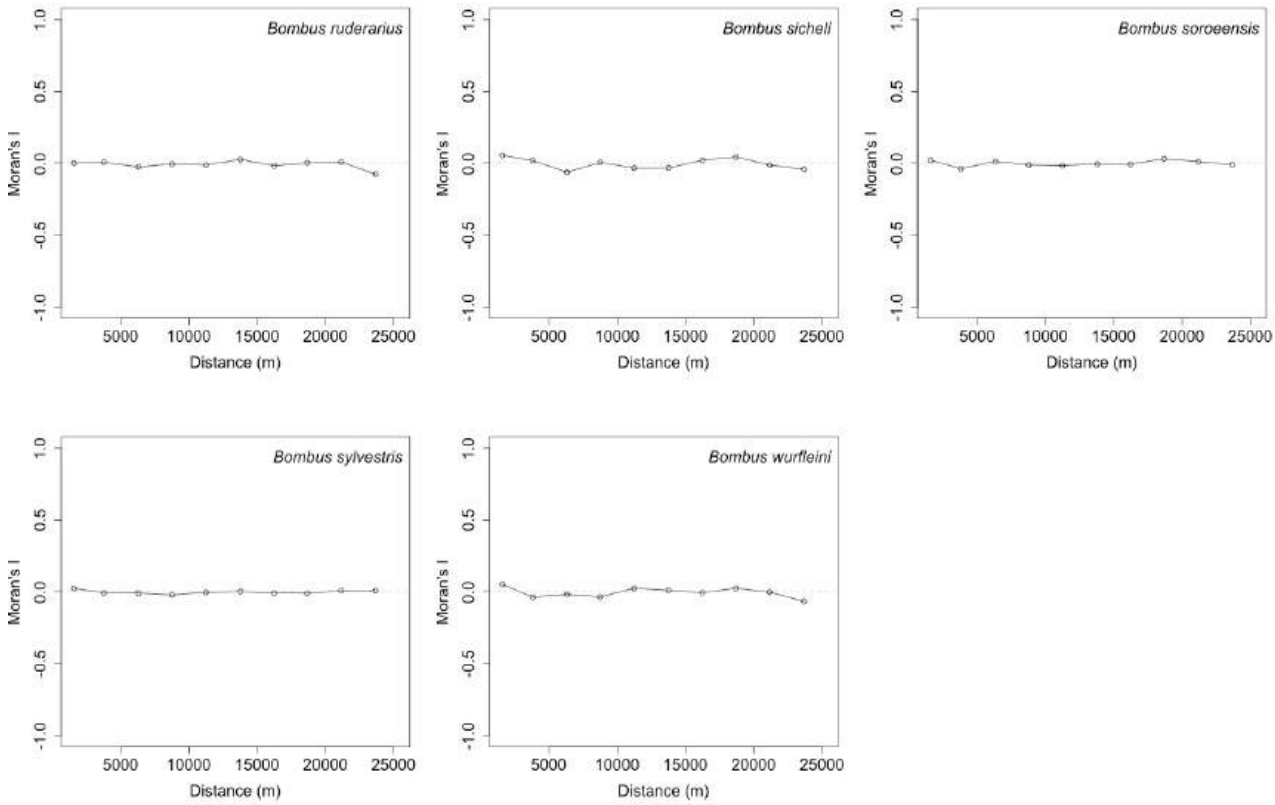


Figure S1 Spatial autocorrelation of each species of the *Bombus* group based on Moran's *I* spatial correlograms. All correlograms are globally significant at the α = 0.05 level since several individual values are significant after Bonferroni correction. Filled symbols are significant values after Holm's correction for multiple testing (α=0.05). Distances up to 2/3 of the maximum distance between two observations are represented.

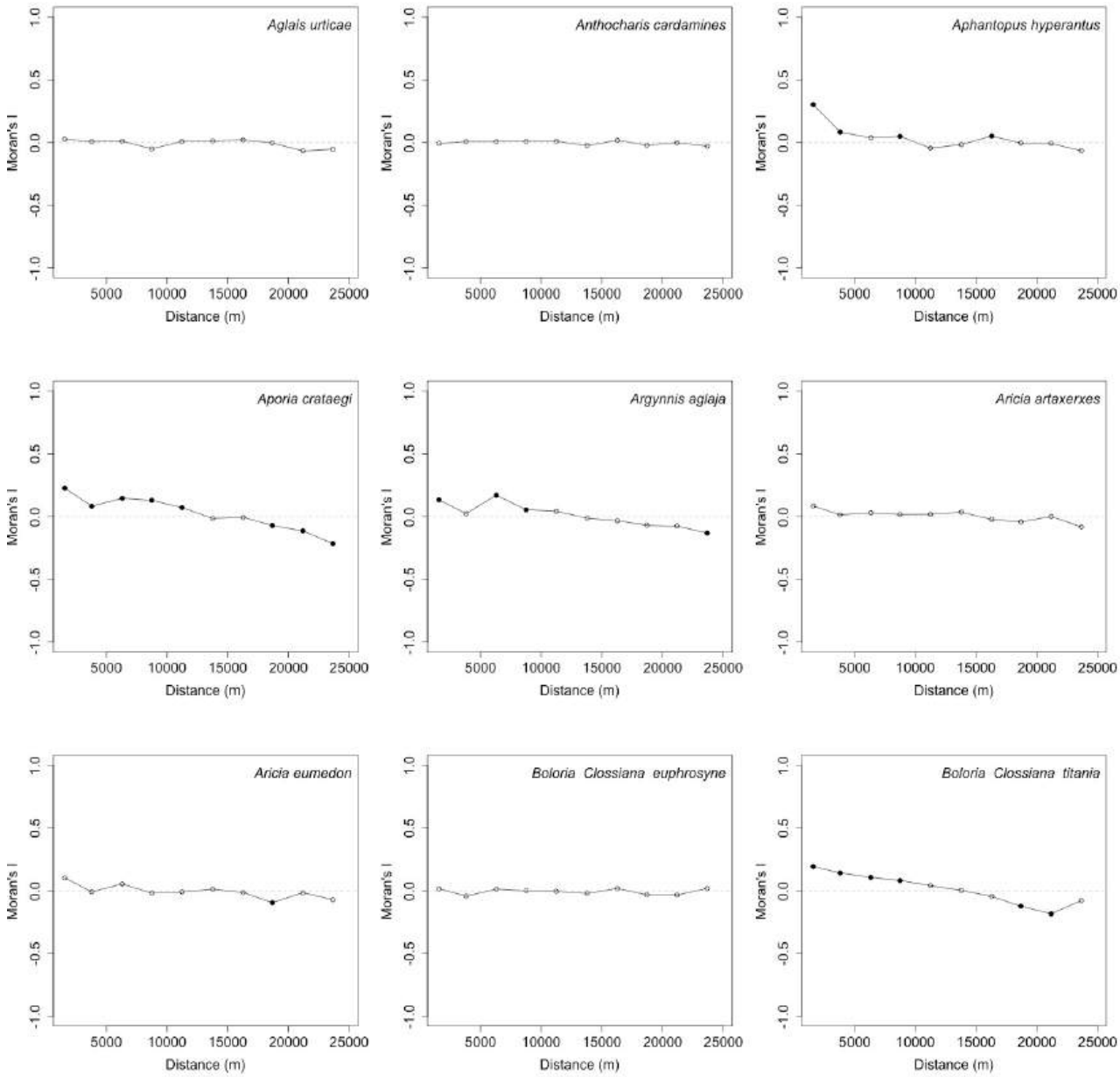


485

486 **Figure S1** Spatial autocorrelation of each species of the *Bombus* group based on Moran's *I* spatial

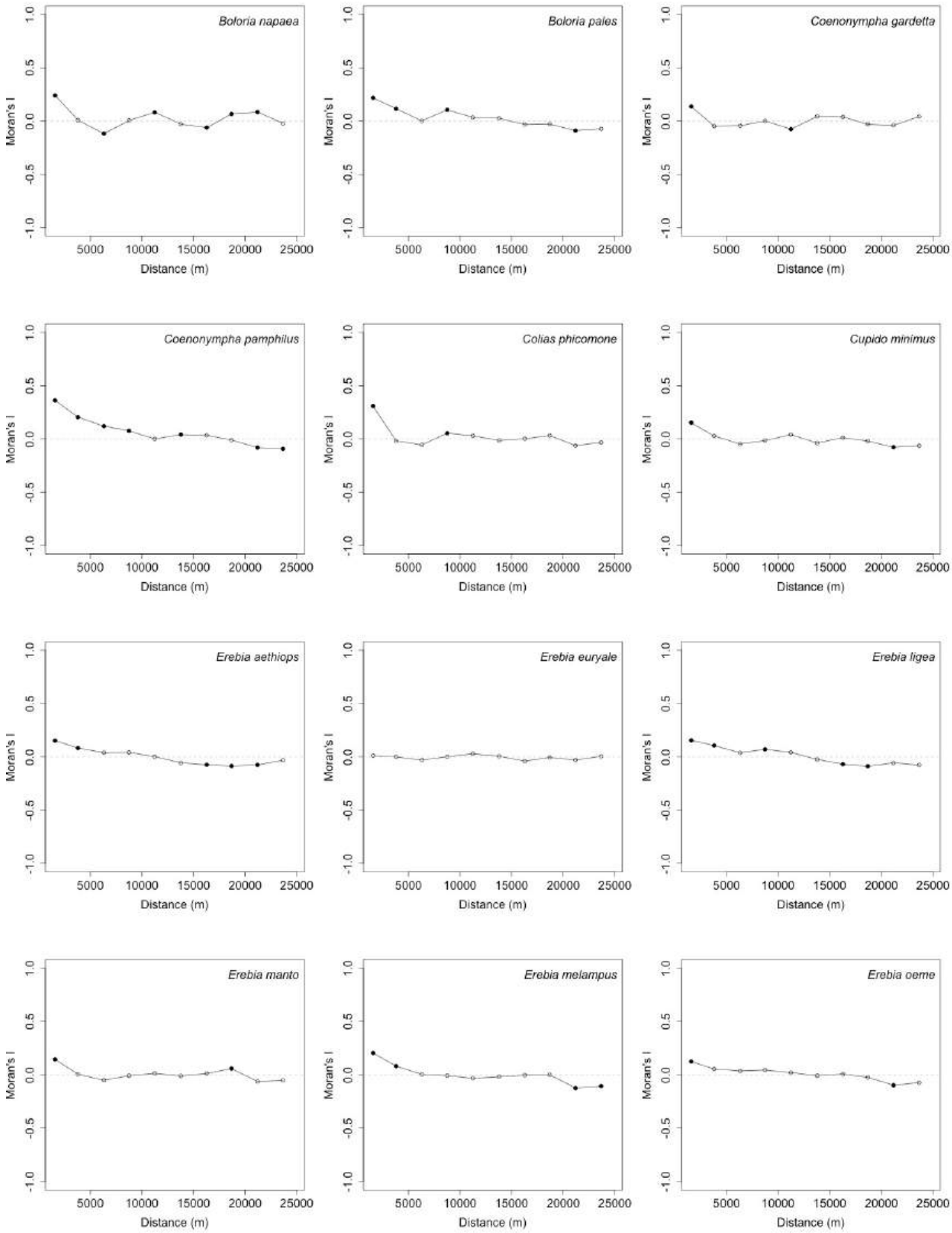
487 correlograms (cont.).

488



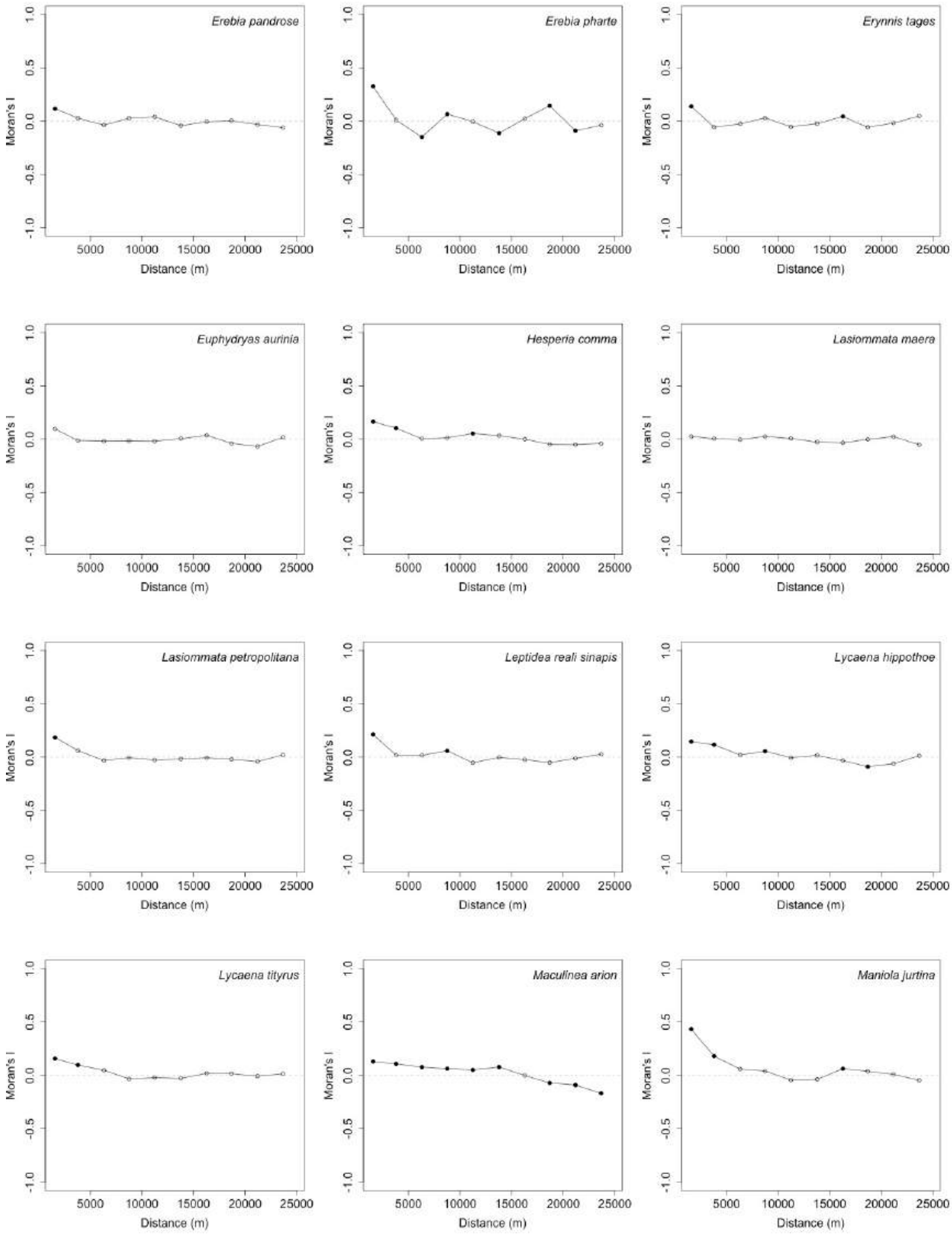
489

490 **Figure S2** Spatial autocorrelation of each species of the *Lepidoptera* group based on Moran's *I* spatial
491 correlograms. All correlograms are globally significant at the α = 0.05 level since several individual values
492 are significant after Bonferroni correction. Filled symbols are significant values after Holm's correction for
493 multiple testing (α=0.05). Distances up to 2/3 of the maximum distance between two observations are
494 represented.



495
496 **Figure S2** Spatial autocorrelation of each species of the *Lepidoptera* group based on Moran's *I* spatial

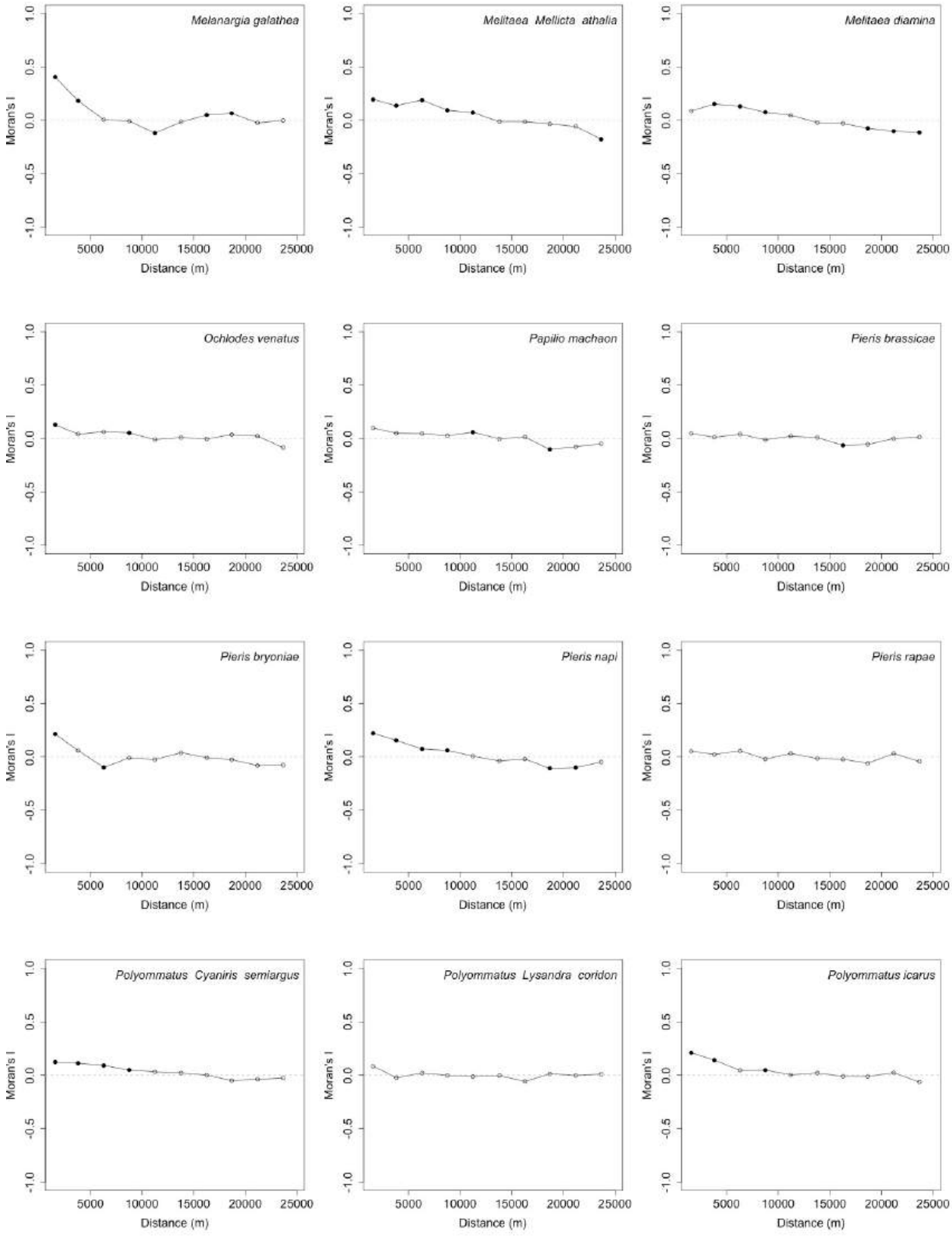
497 correlograms (cont.).



498

499 **Figure S2** Spatial autocorrelation of each species of the *Lepidoptera* group based on Moran's *I* spatial

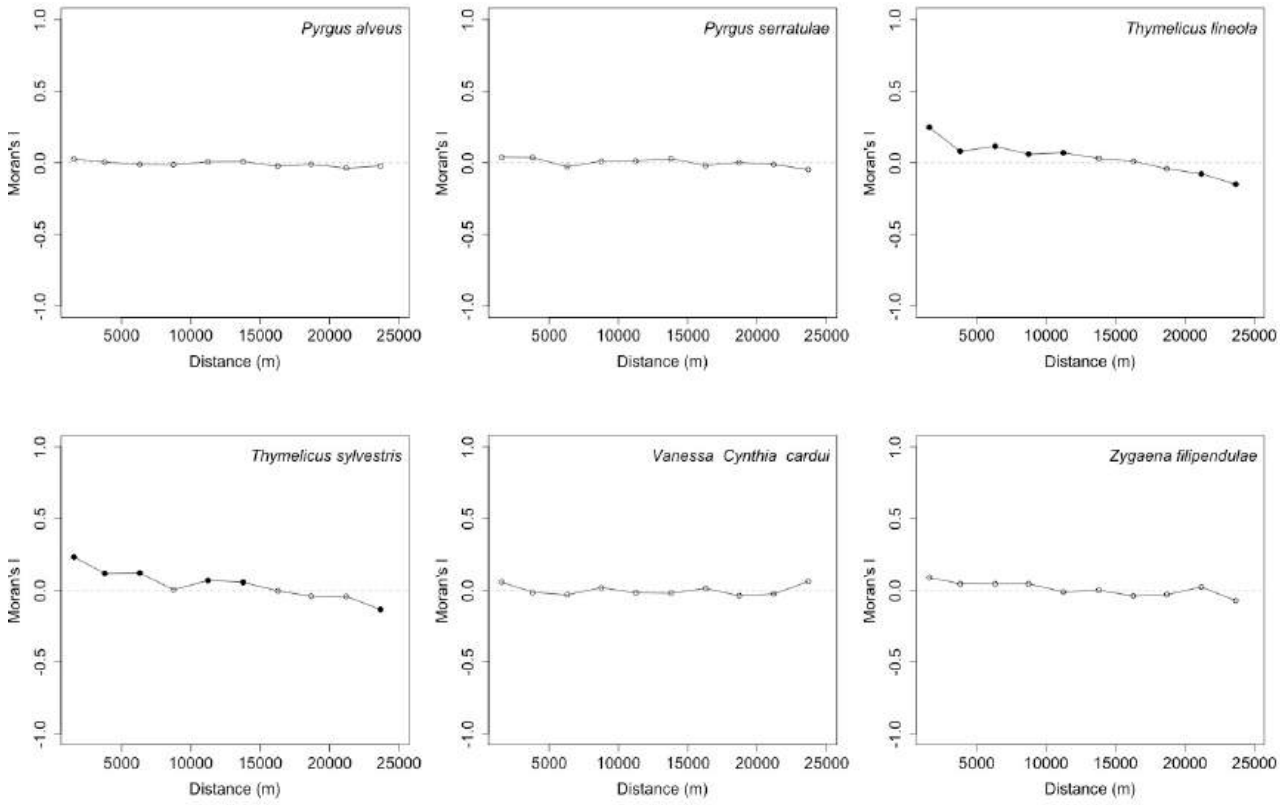
500 correlograms (cont.).



501

502 **Figure S2** Spatial autocorrelation of each species of the *Lepidoptera* group based on Moran's *I* spatial

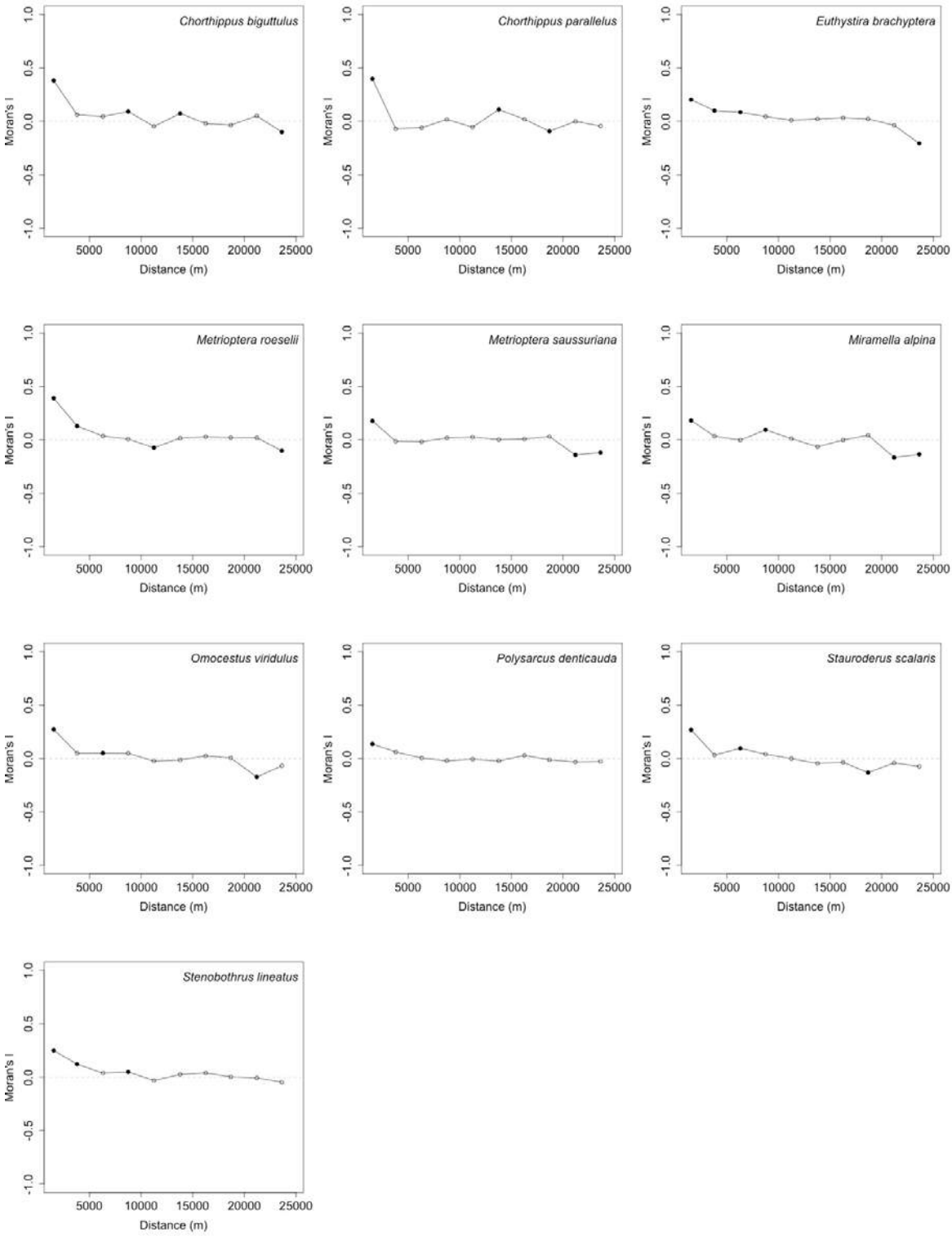
503 correlograms (cont.).



504

505 **Figure S2** Spatial autocorrelation of each species of the *Lepidoptera* group based on Moran's *I* spatial

506 correlograms (cont.).



507

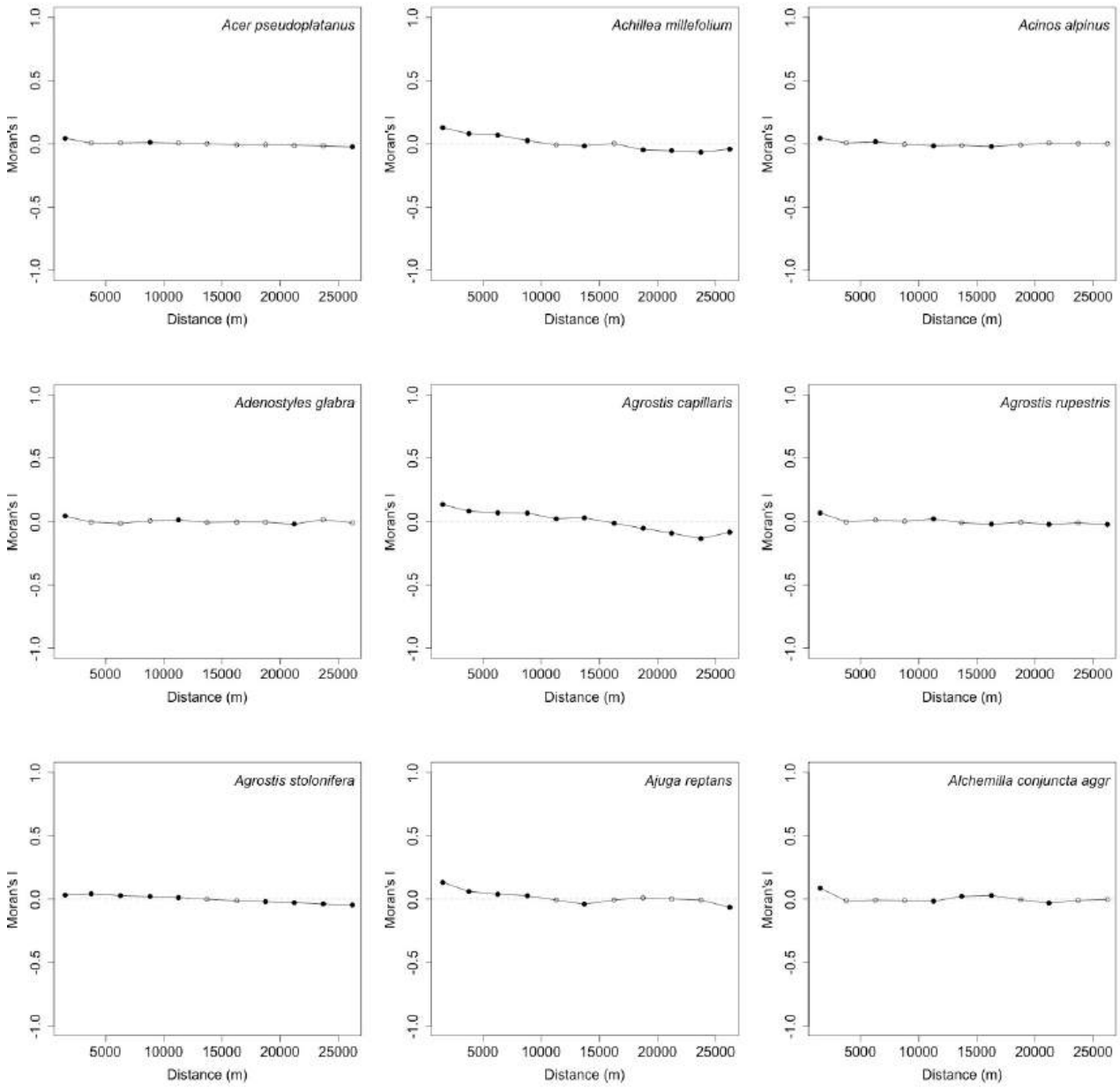
508 **Figure S3** Spatial autocorrelation of each species of the *Orthoptera* group based on Moran's *I* spatial

509 correlograms. All correlograms are globally significant at the α = 0.05 level since several individual values

510 are significant after Bonferroni correction. Filled symbols are significant values after Holm's correction for

511 multiple testing (α=0.05). Distances up to 2/3 of the maximum distance between two observations are

512 represented.



513

514 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

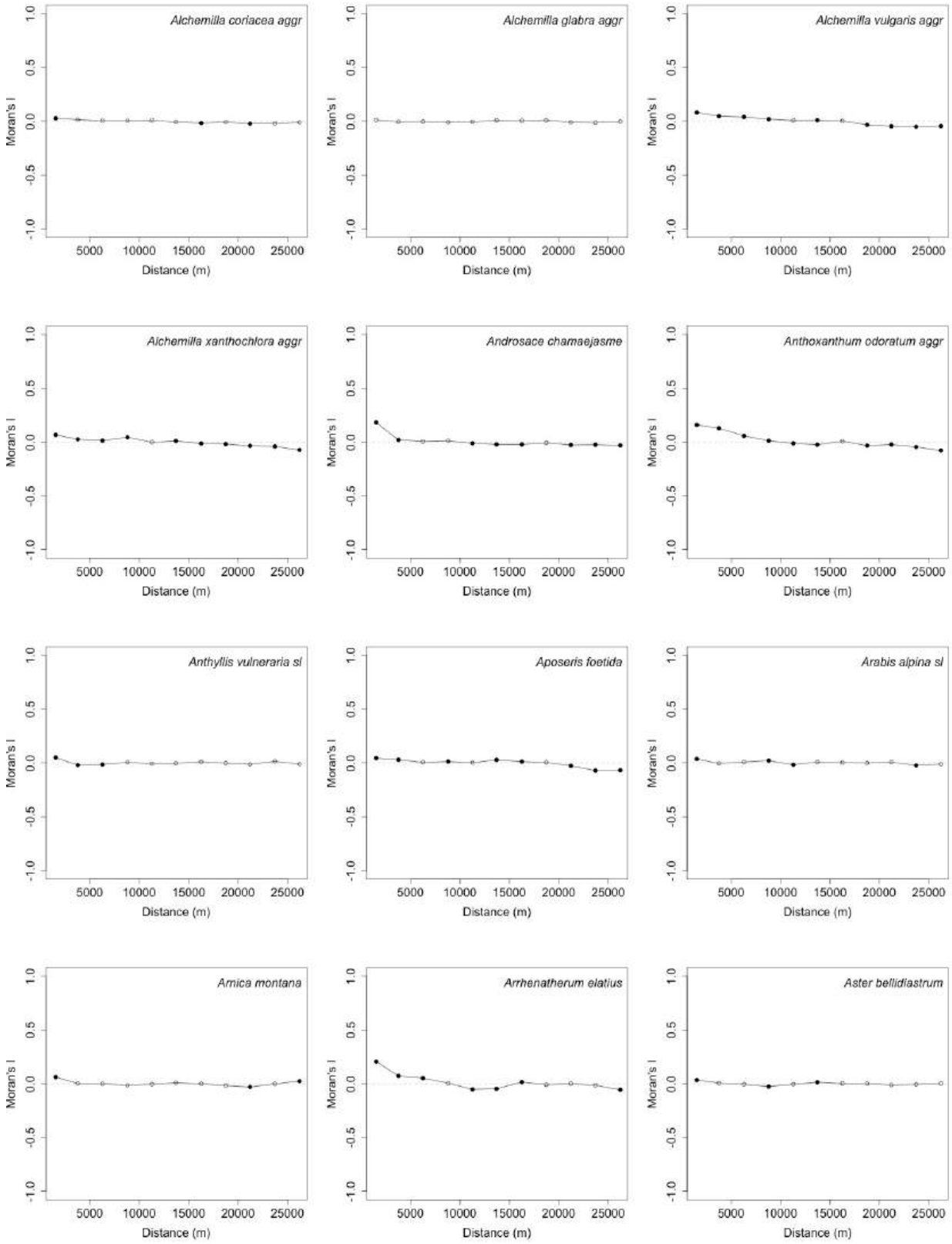
515 correlograms. All correlograms are globally significant at the α = 0.05 level since several individual values

516 are significant after Bonferroni correction. Filled symbols are significant values after Holm's correction for

517 multiple testing (α=0.05). Distances up to 2/3 of the maximum distance between two observations are

518 represented.

519



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521 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

522 correlograms (cont.).

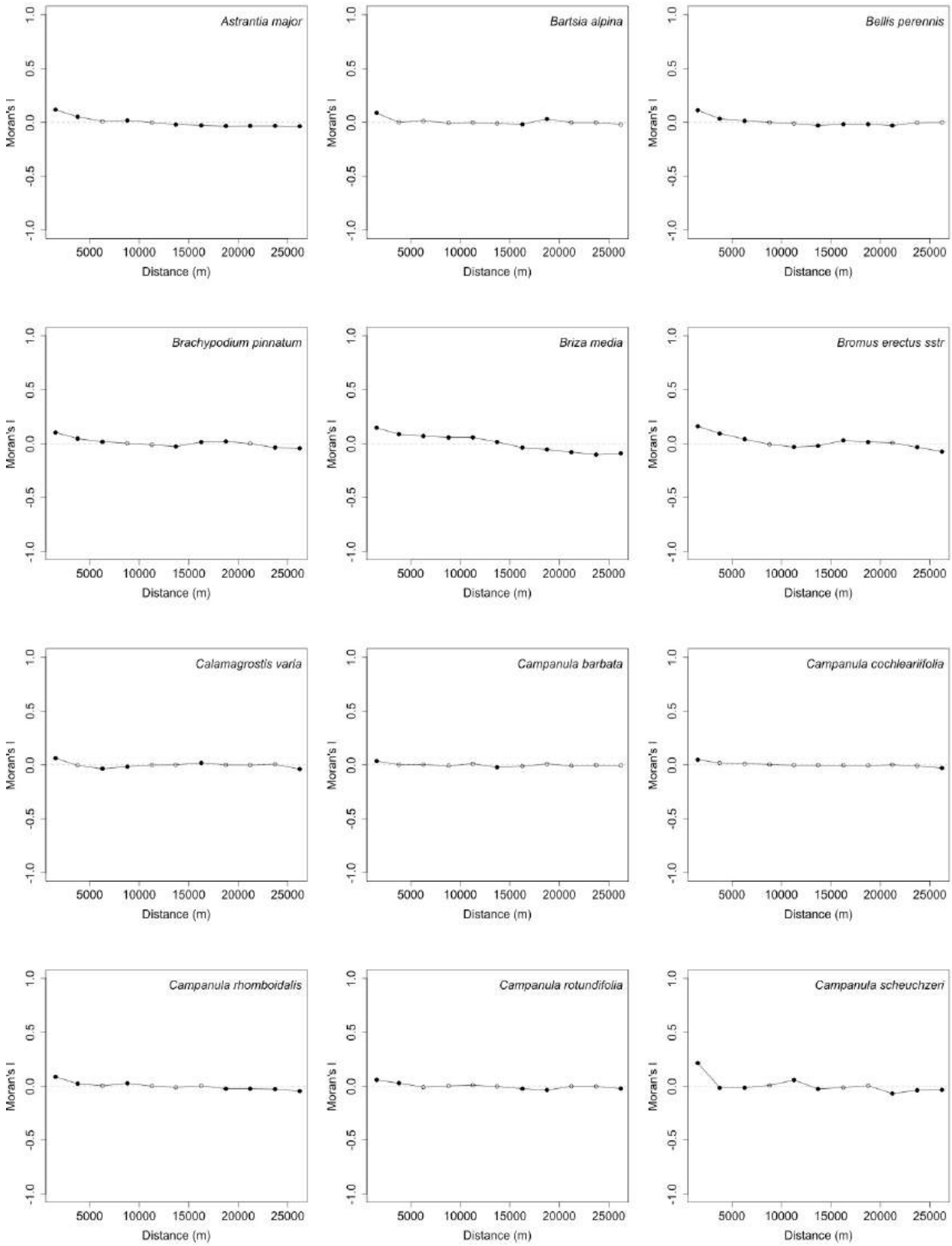
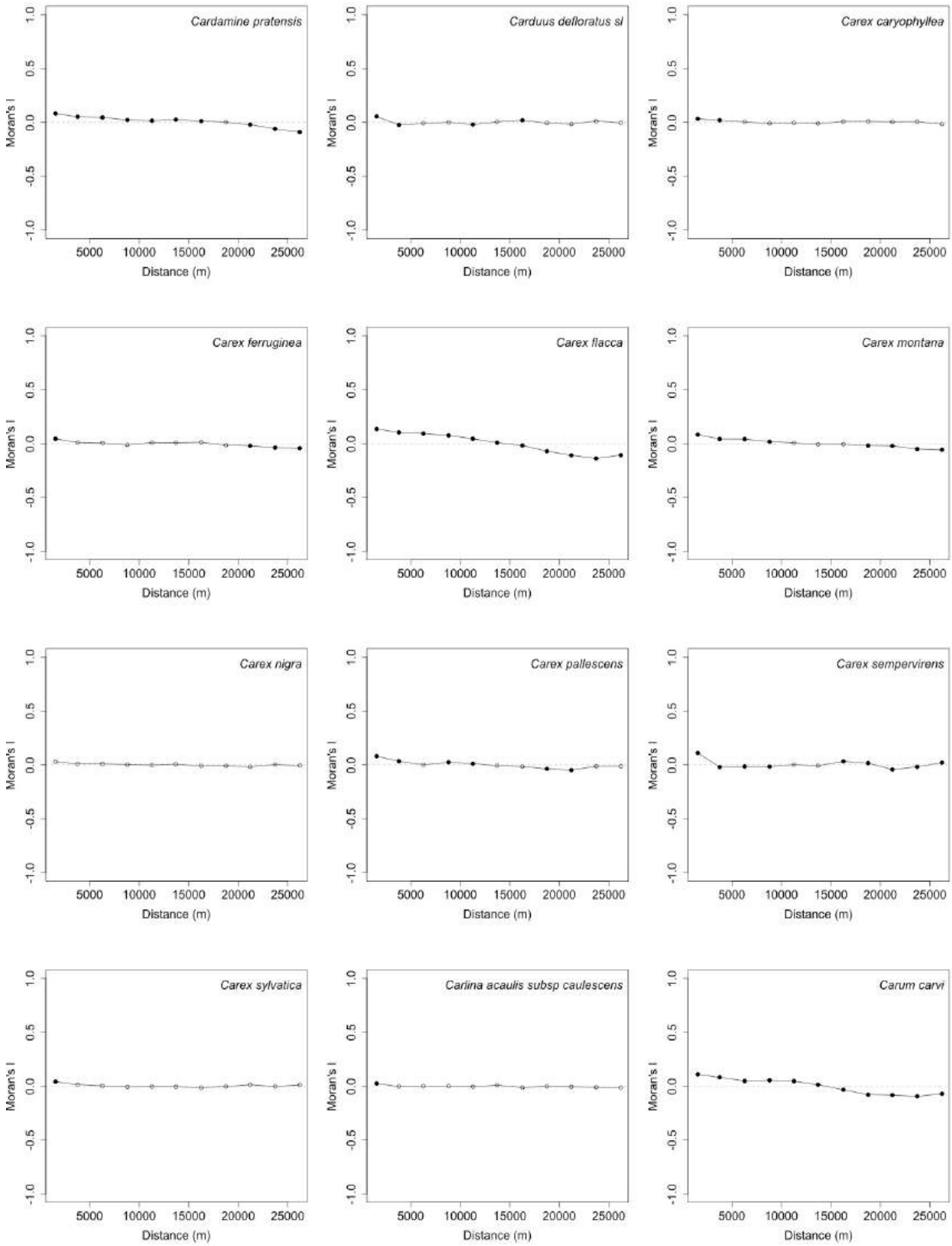


Figure S4 Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial correlograms (cont.).



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527 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

528 correlograms (cont.).

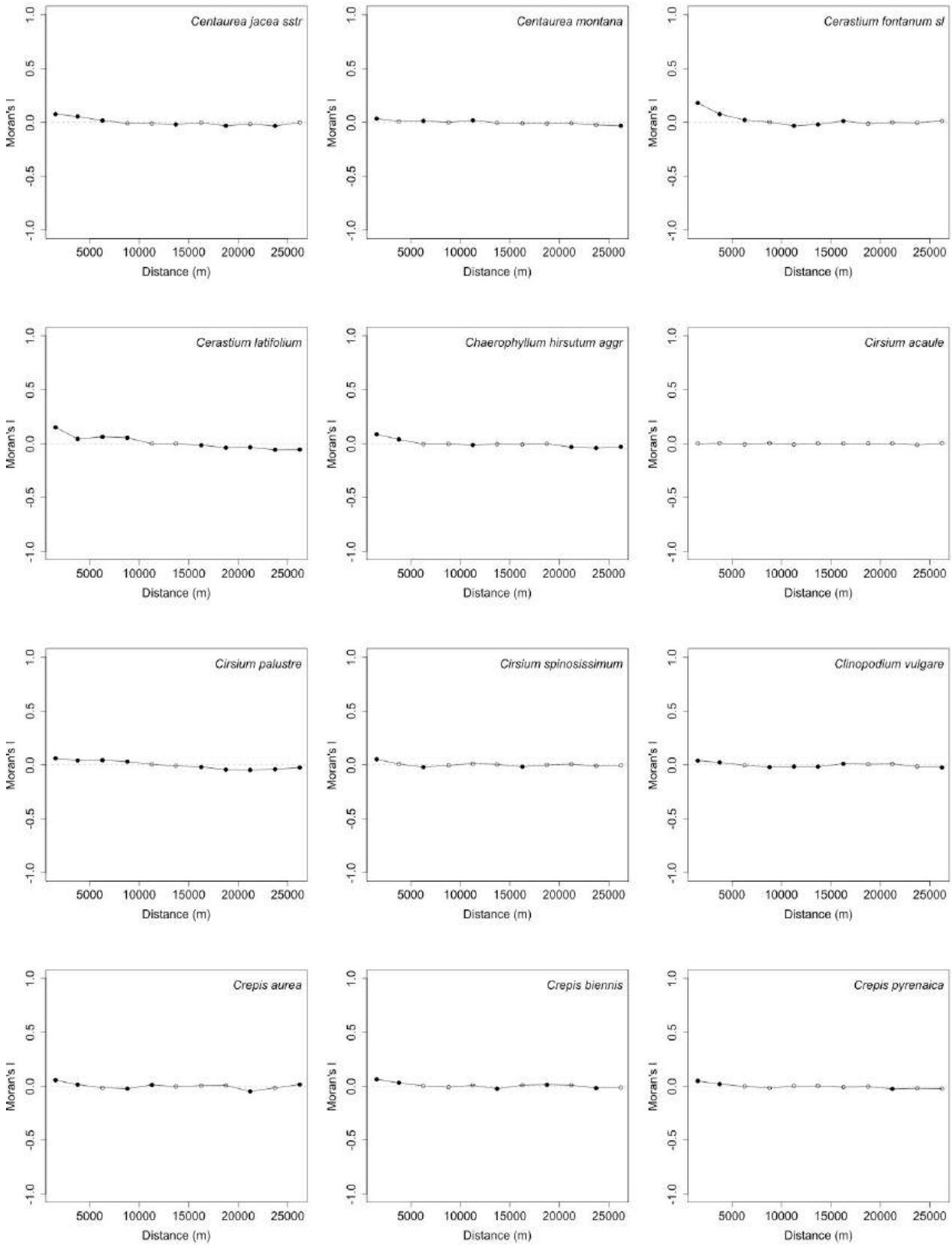
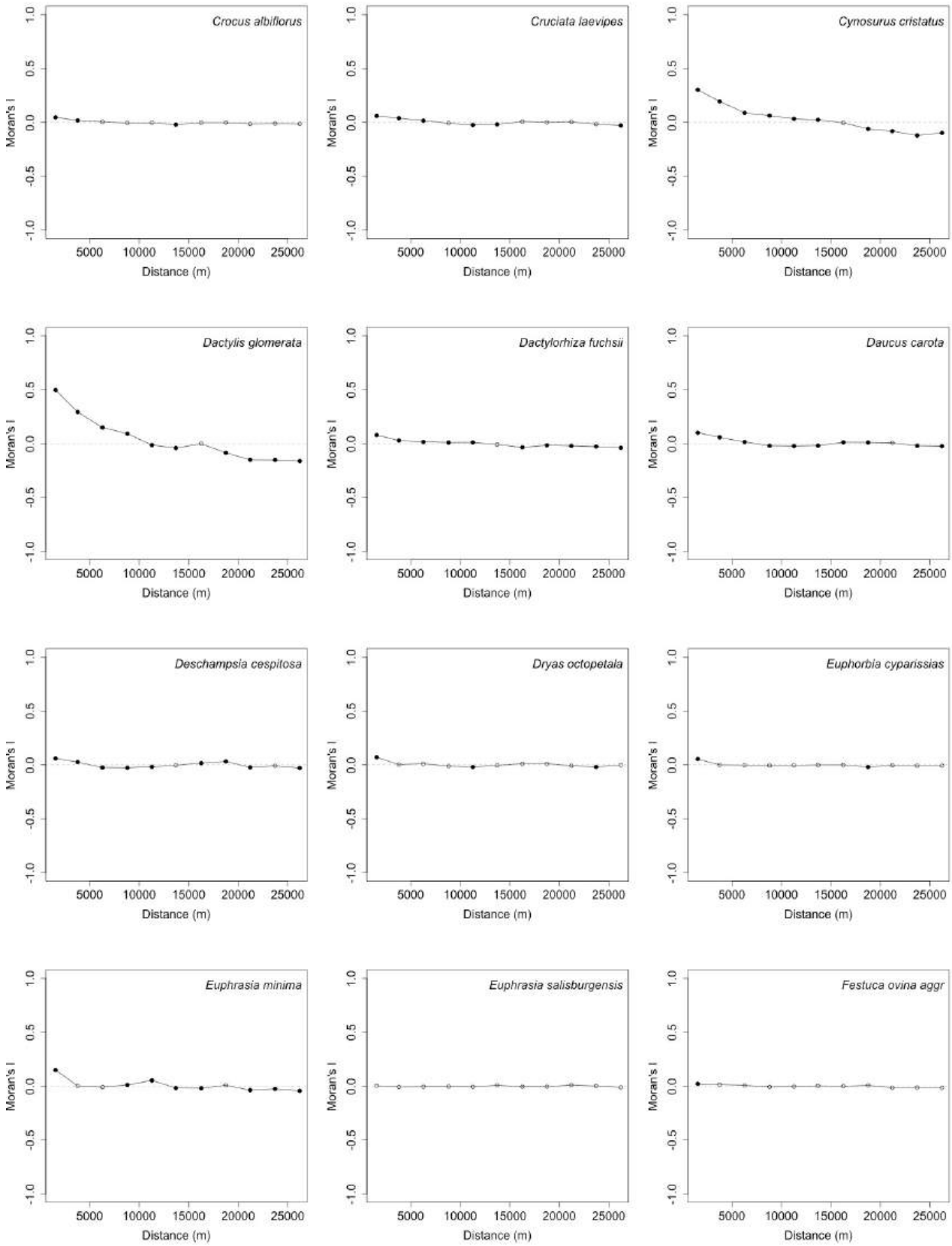


Figure S4 Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial correlograms (cont.).



532

533 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

534 correlograms (cont.).

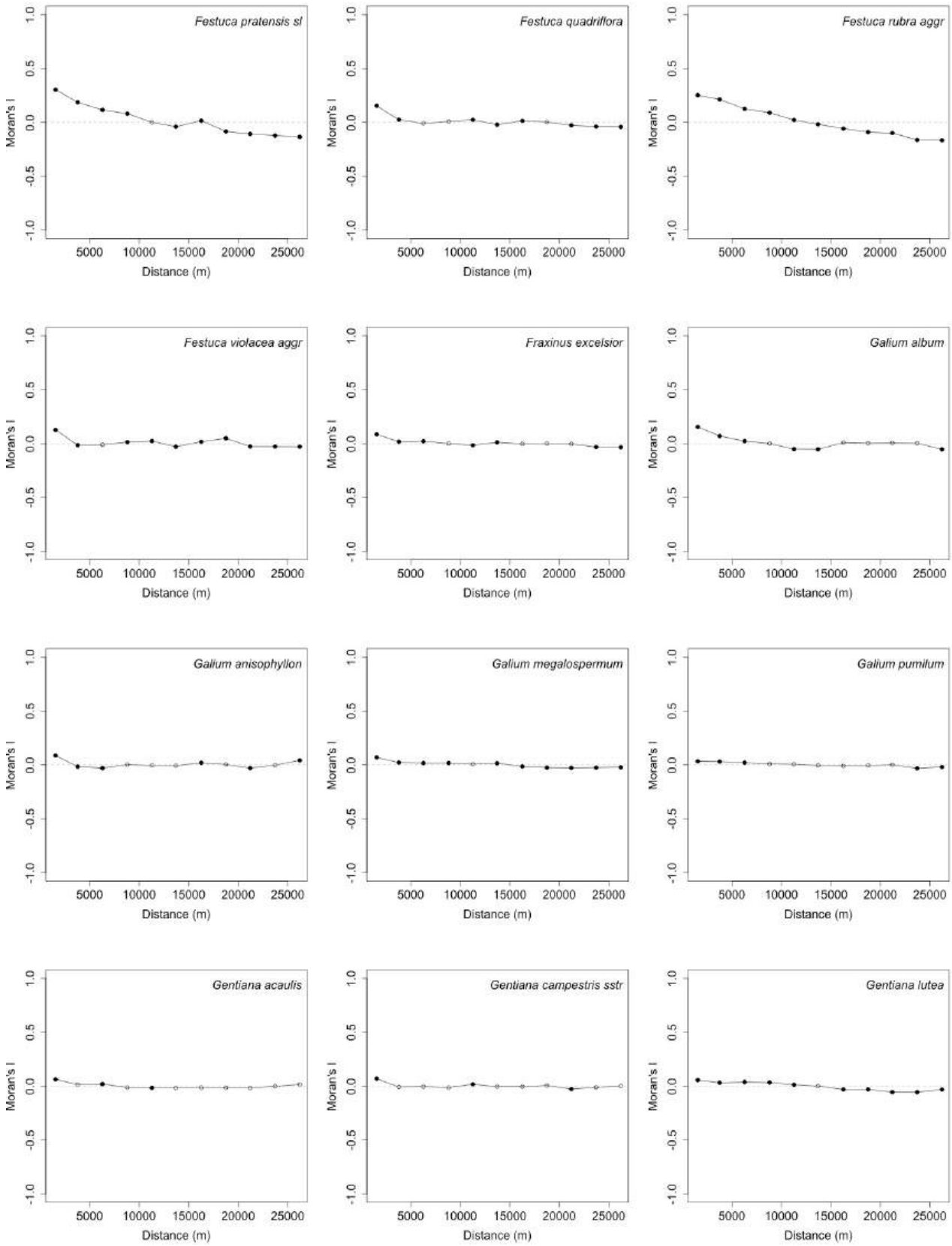
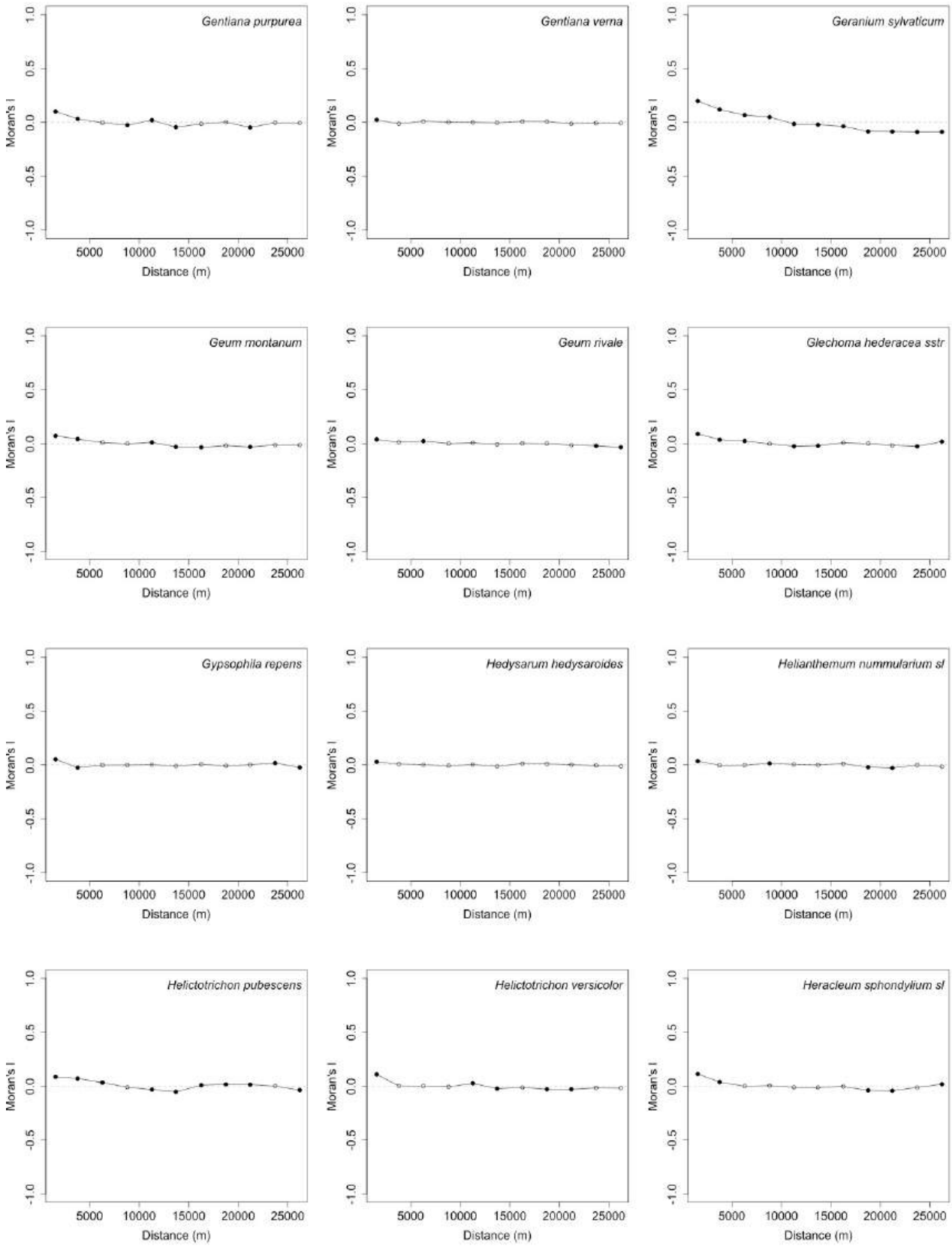


Figure S4 Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial correlograms (cont.).



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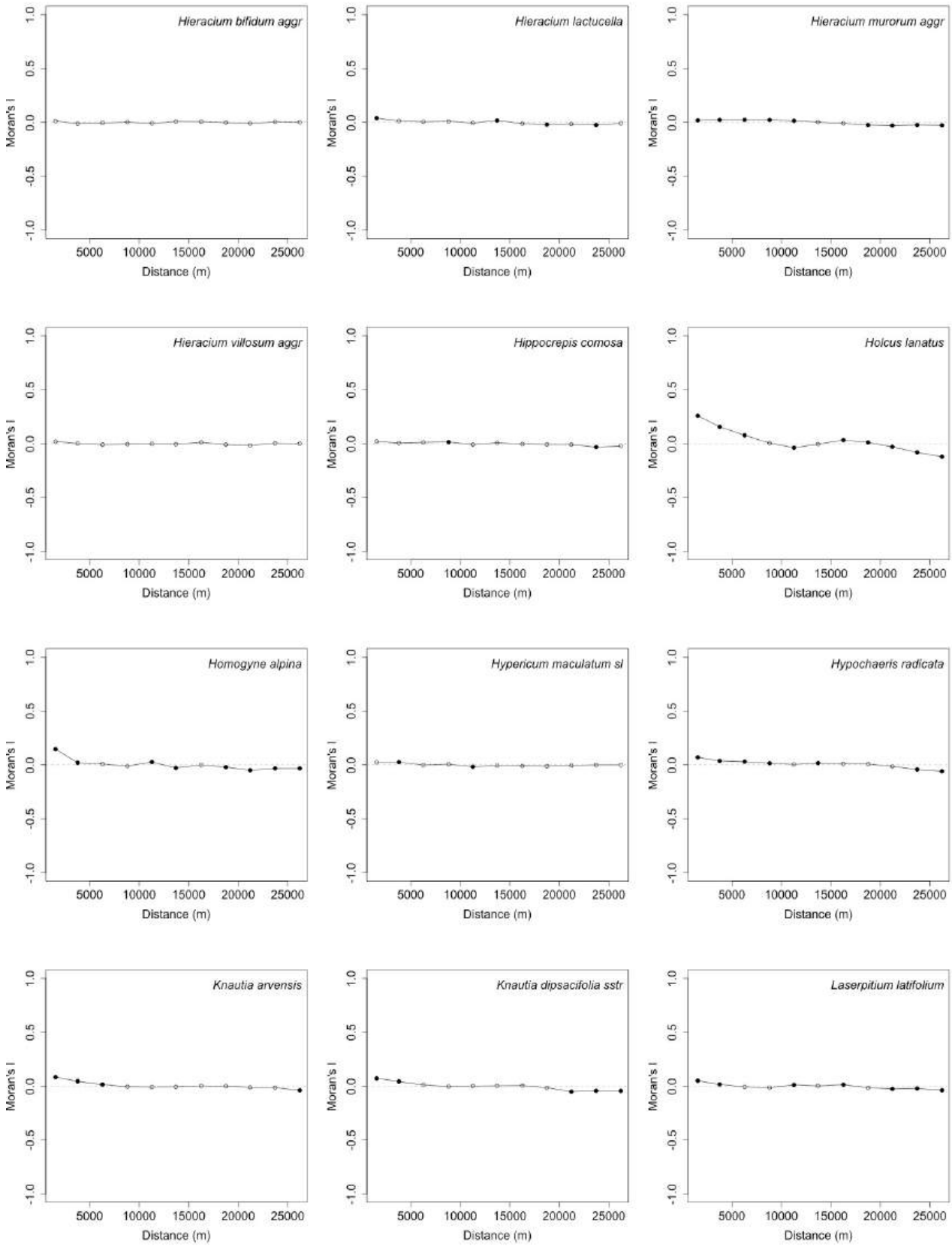
539 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

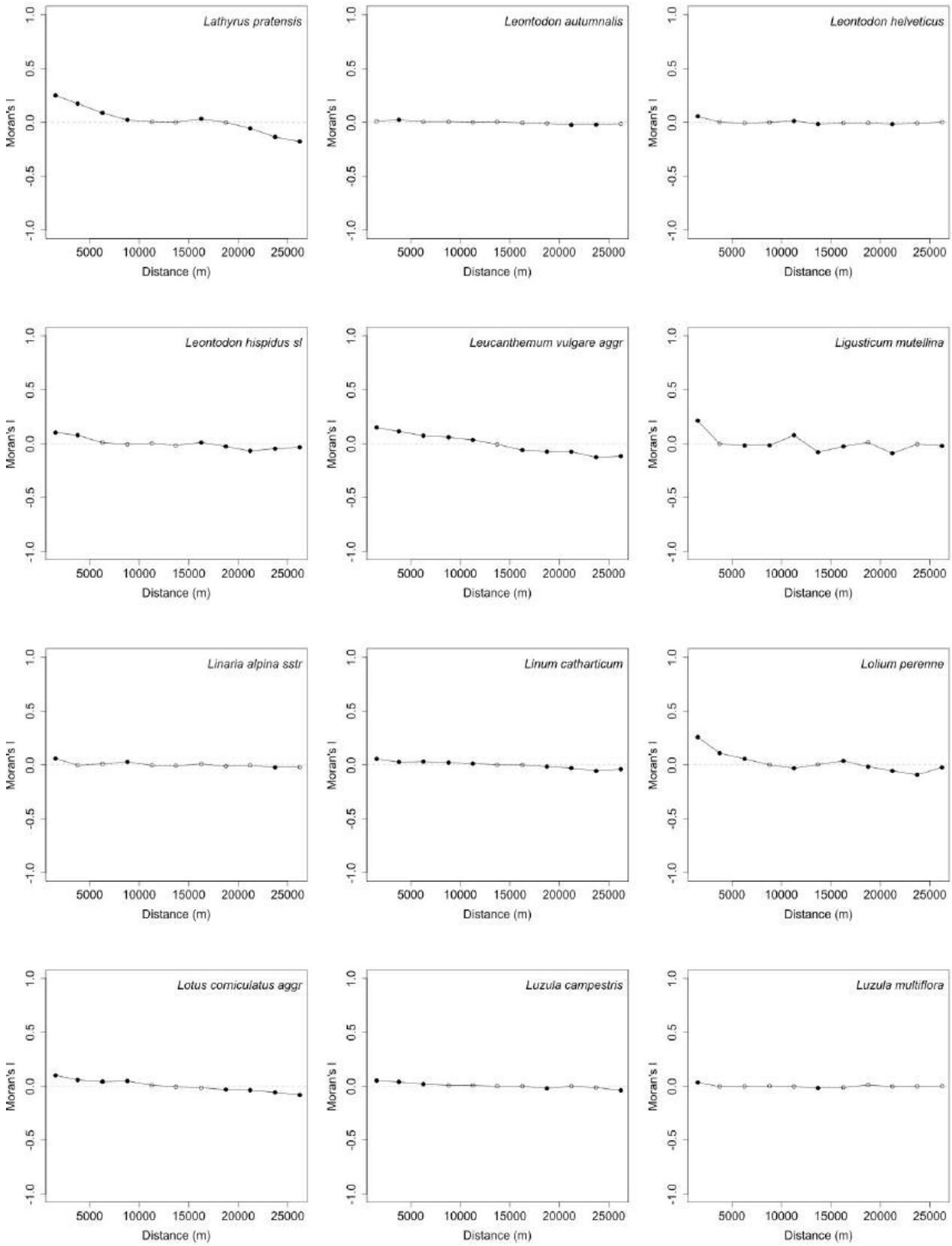
540 correlograms (cont.).



541

542 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

543 correlograms (cont.).



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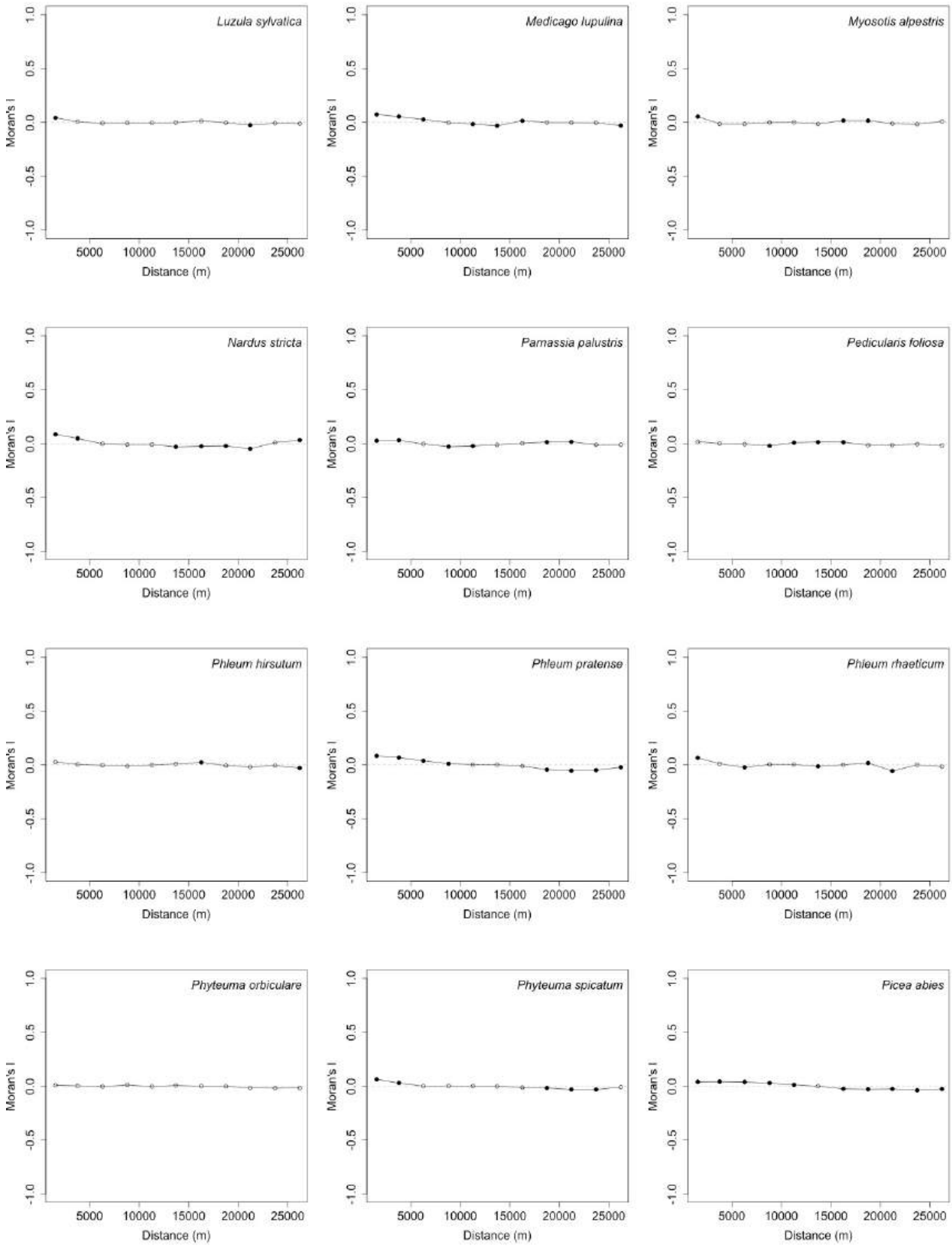
545 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

546 correlograms (cont.).



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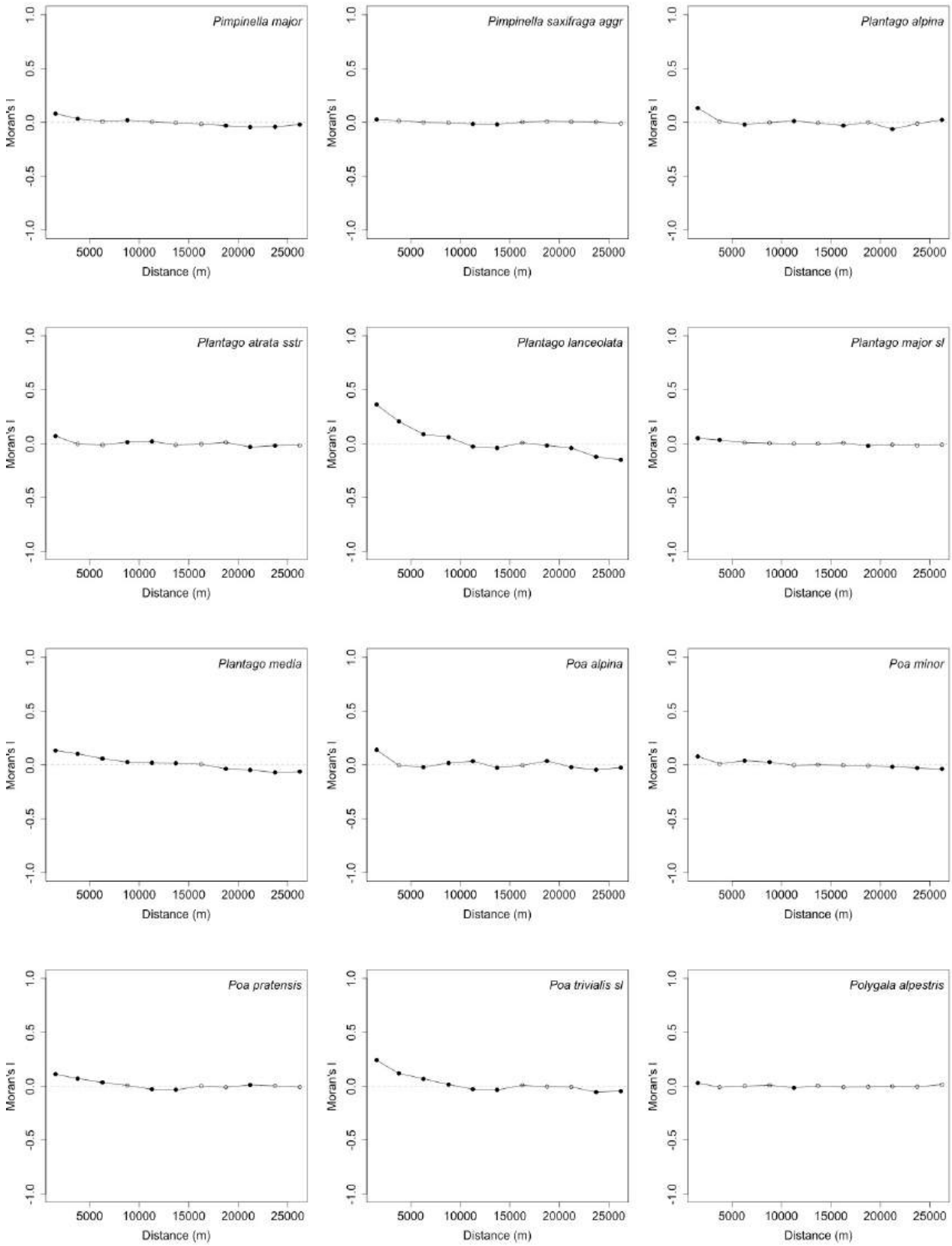
548 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

549 correlograms (cont.).



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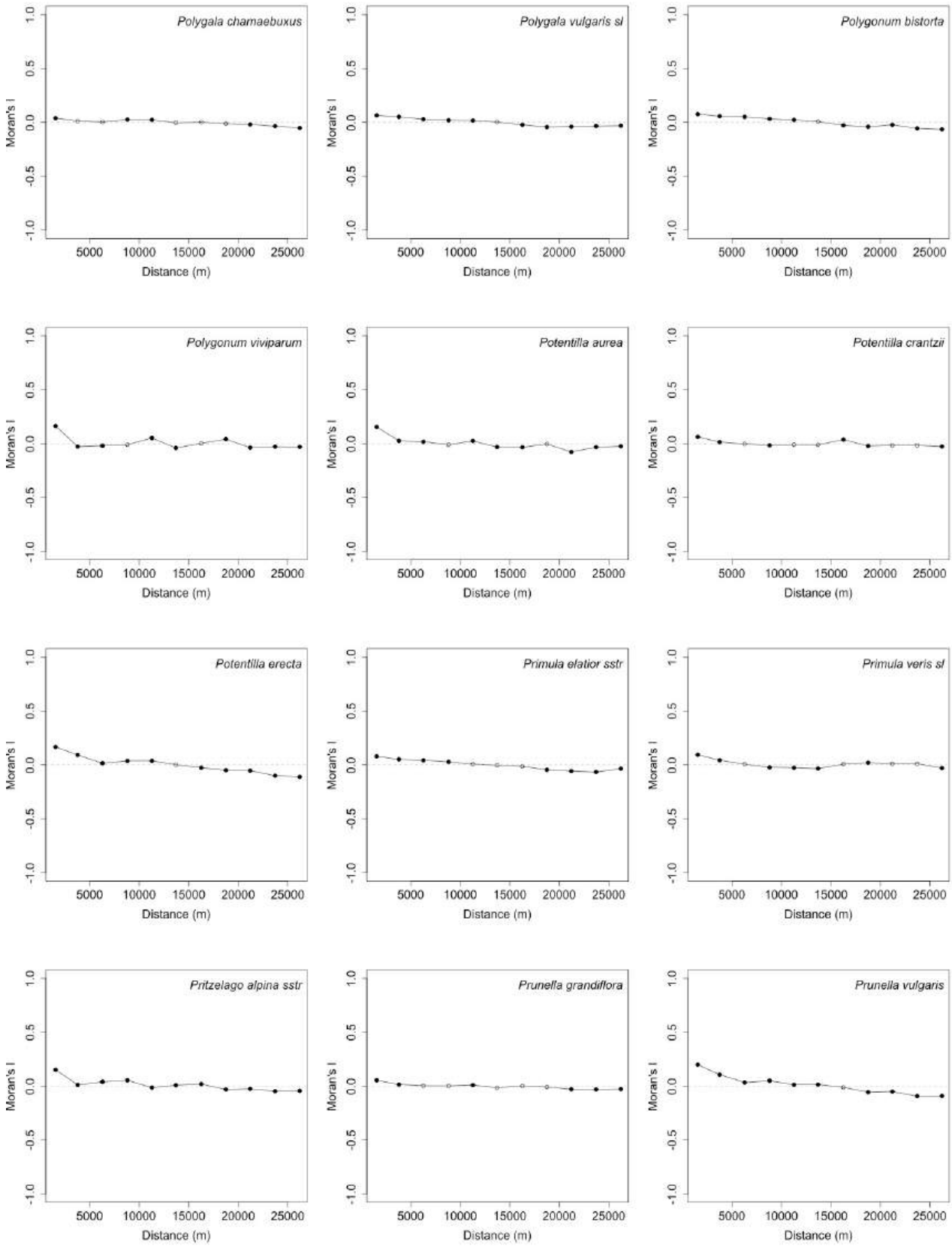
551 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

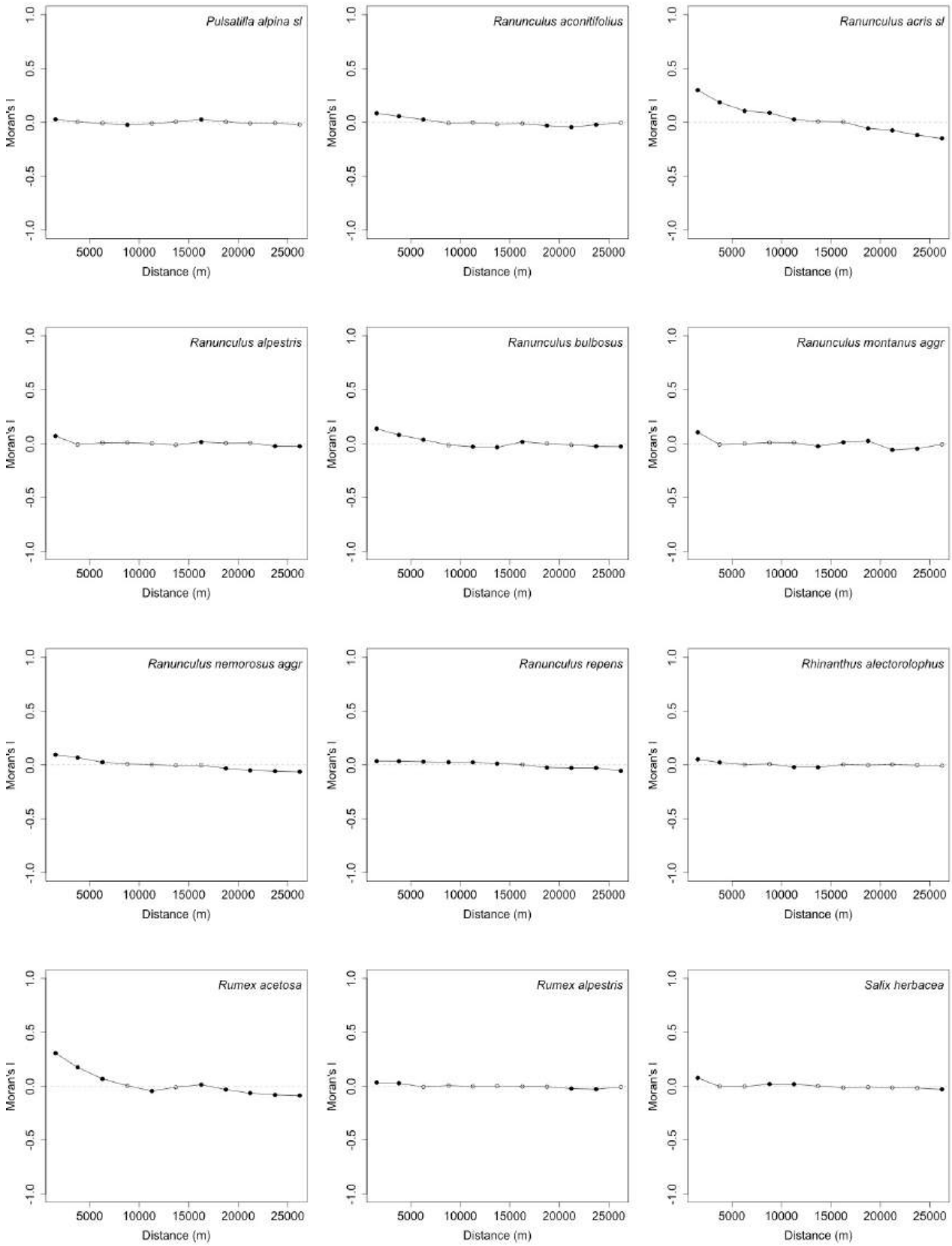
552 correlograms (cont.).



553

554 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

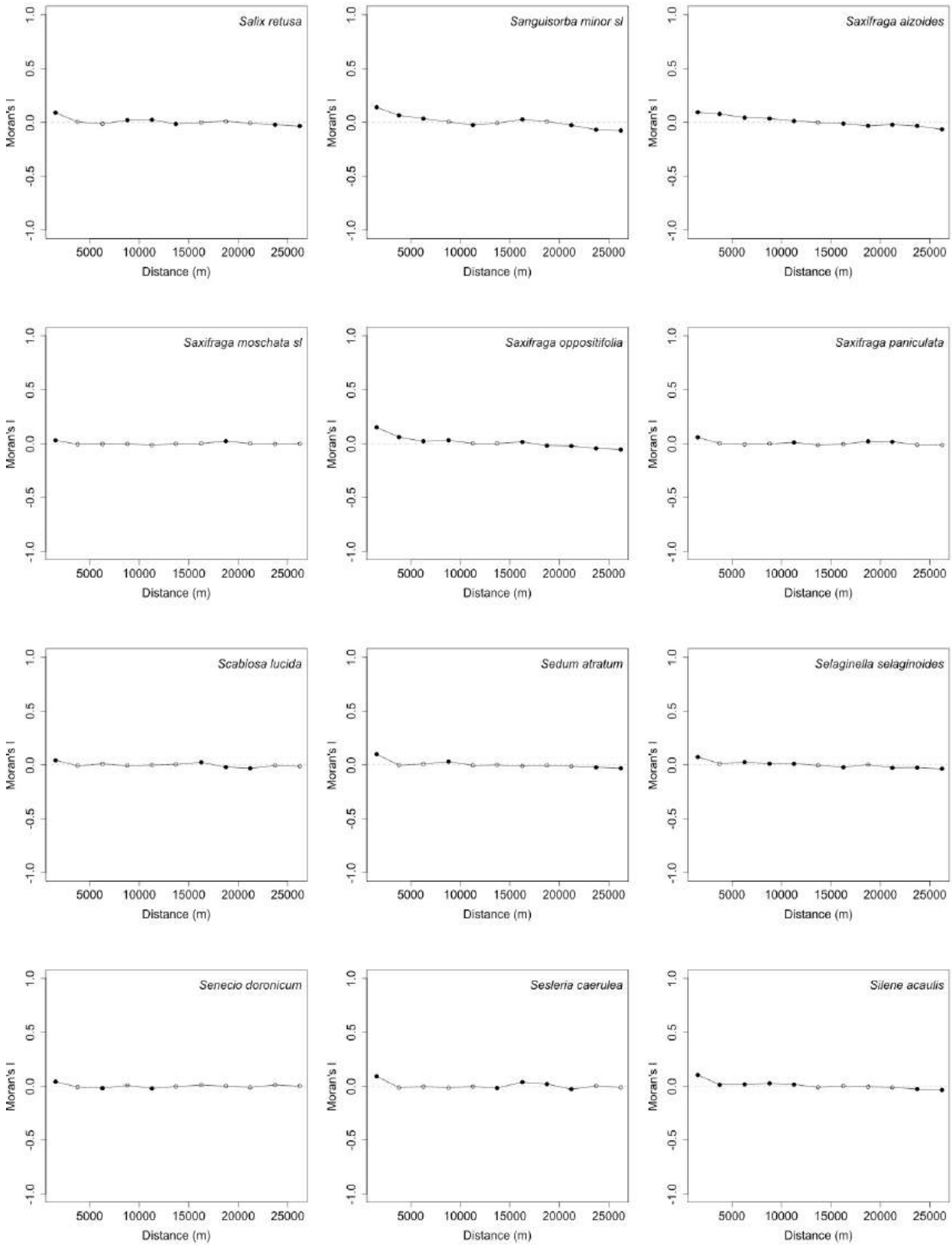
555 correlograms (cont.).



556

557 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

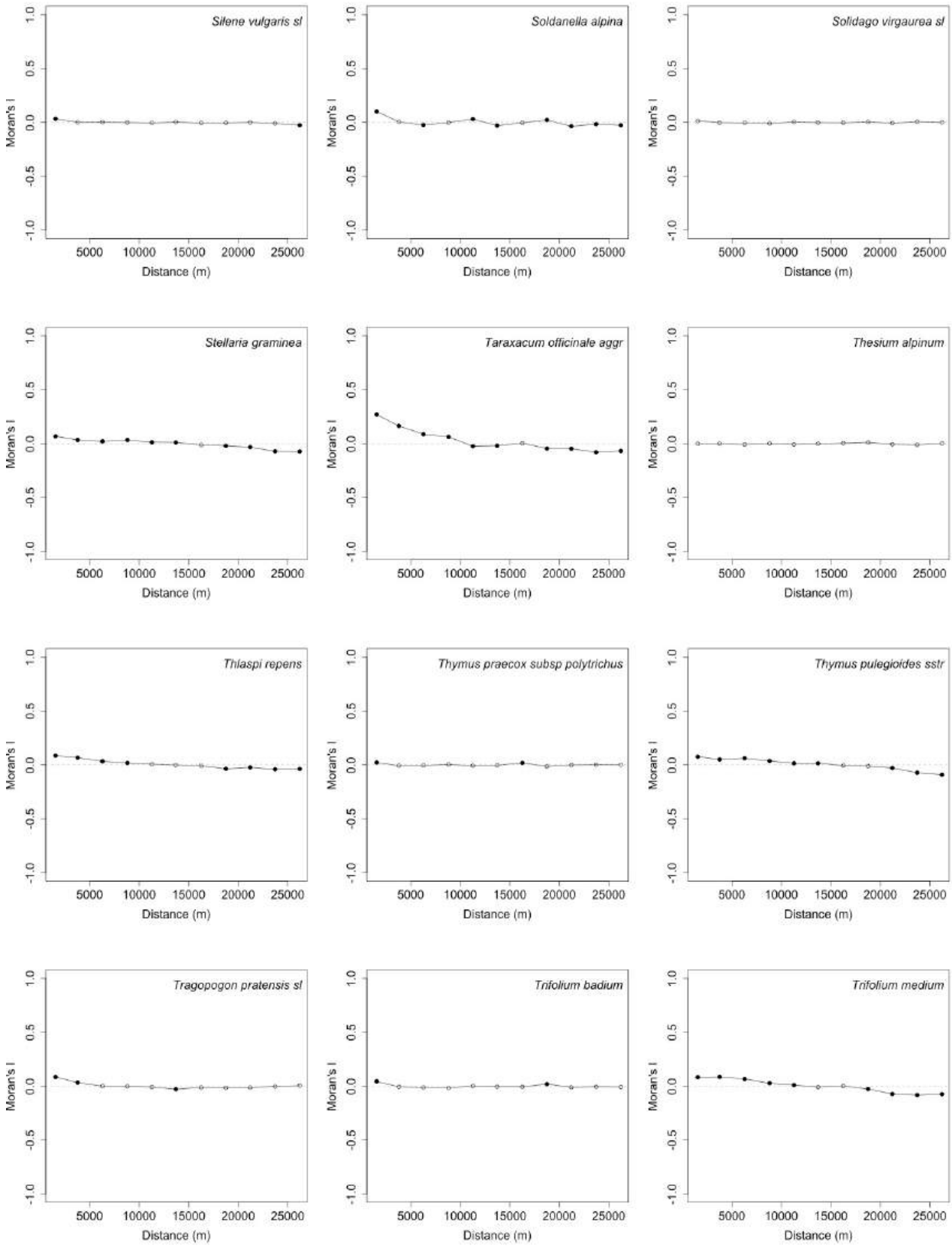
558 correlograms (cont.).



559

560 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

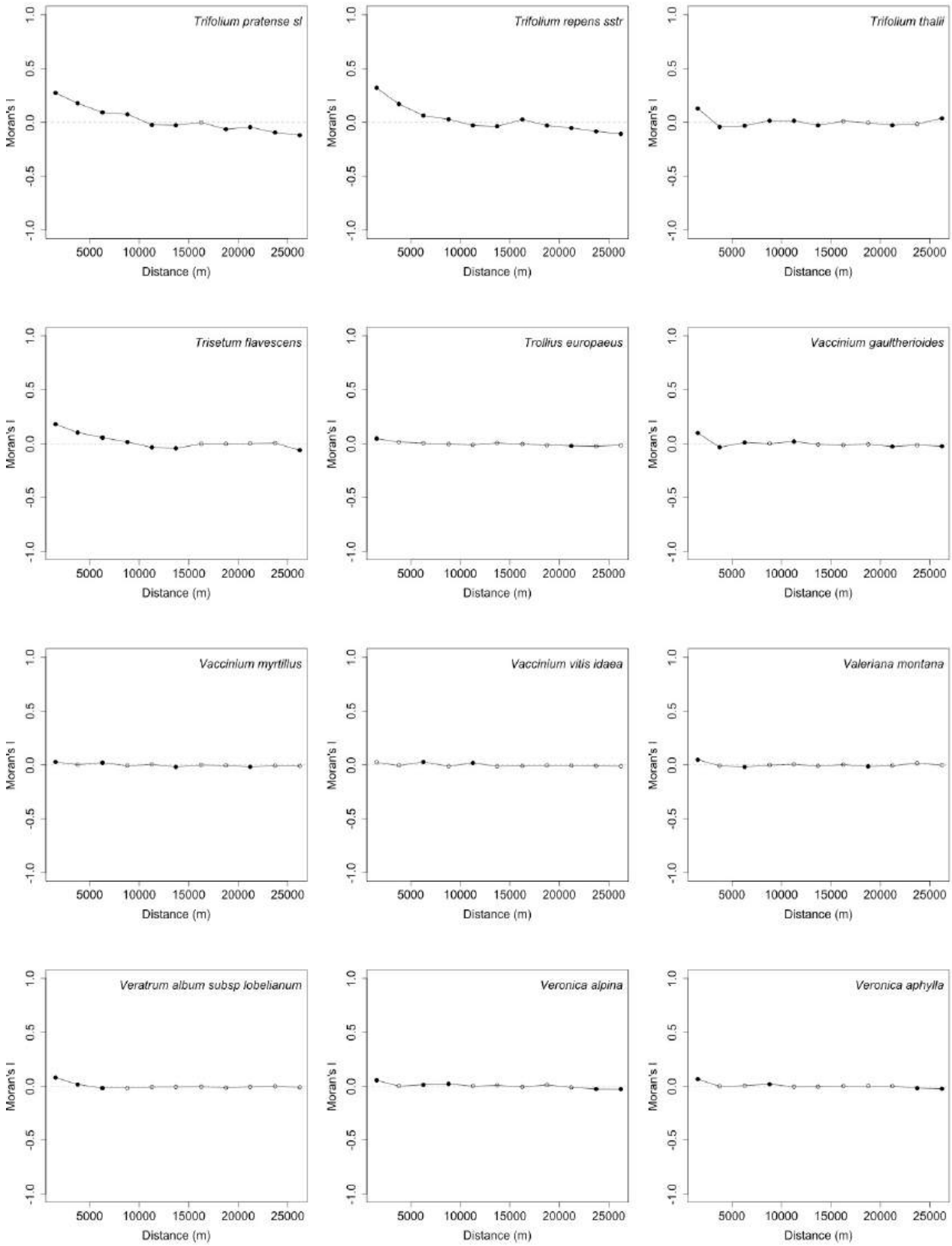
561 correlograms (cont.).



562

563 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

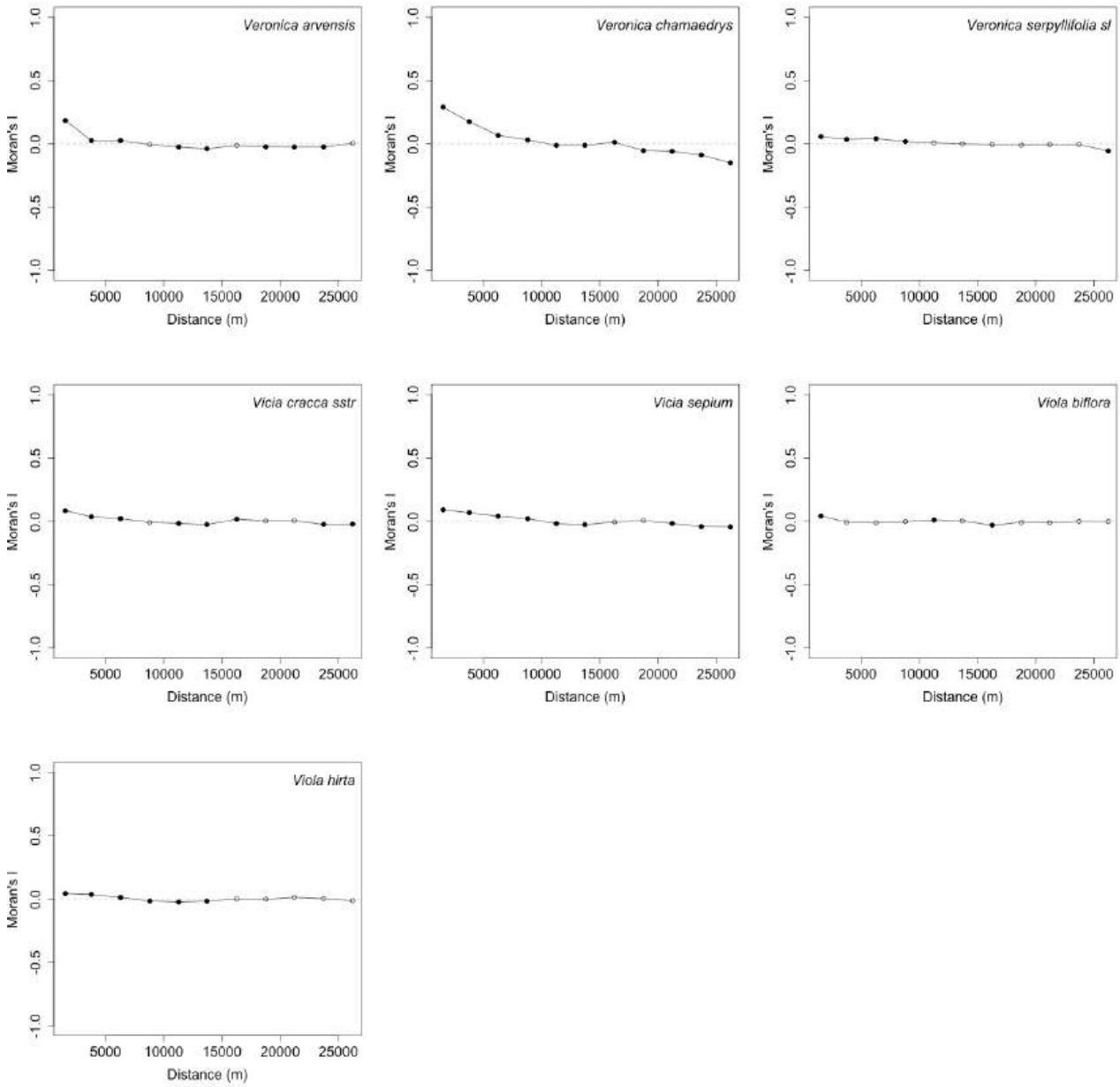
564 correlograms (cont.).



565

566 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

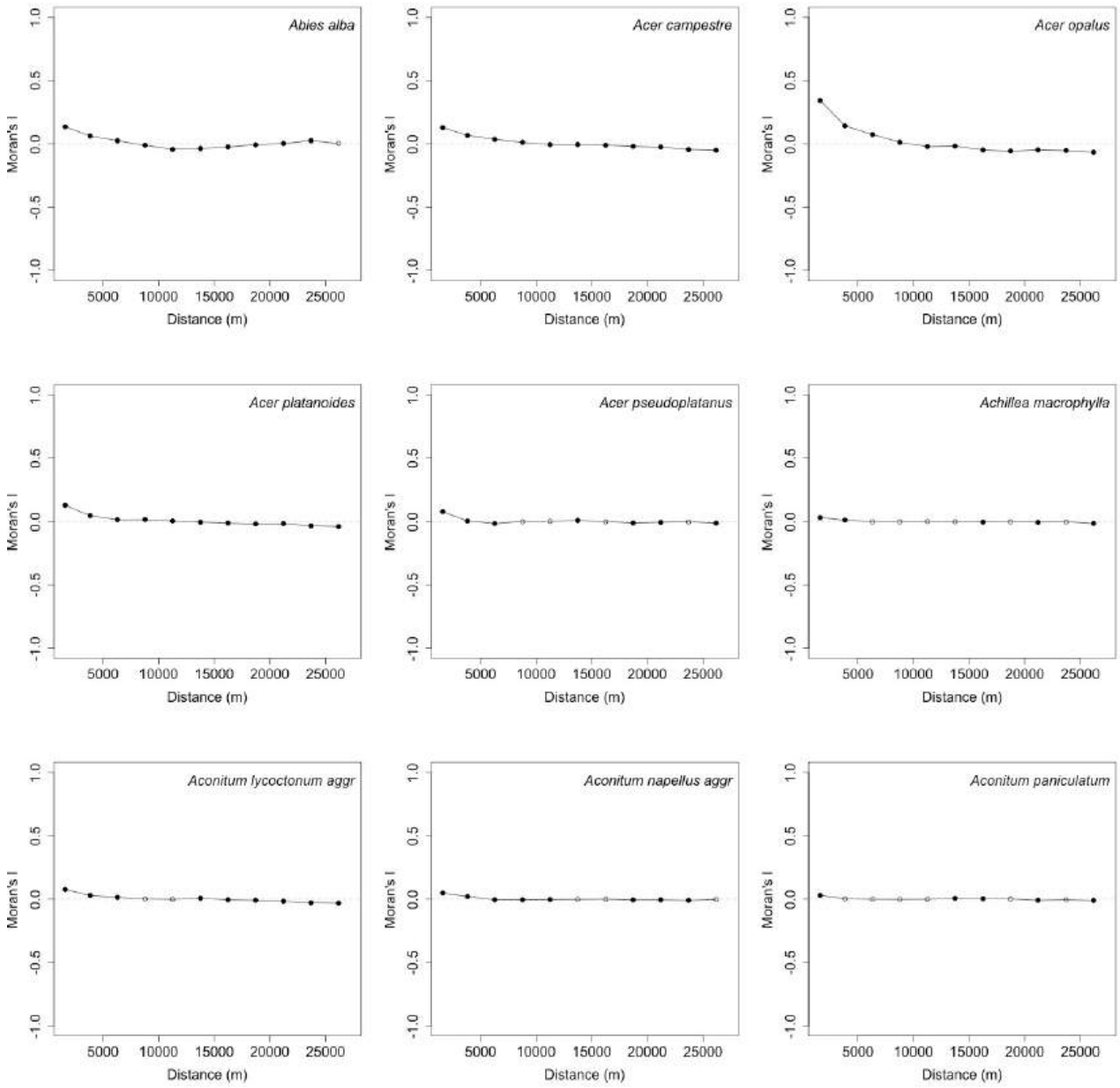
567 correlograms (cont.).



568

569 **Figure S4** Spatial autocorrelation of each species of the *Vegetation* group based on Moran's *I* spatial

570 correlograms (cont.).



571

572 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

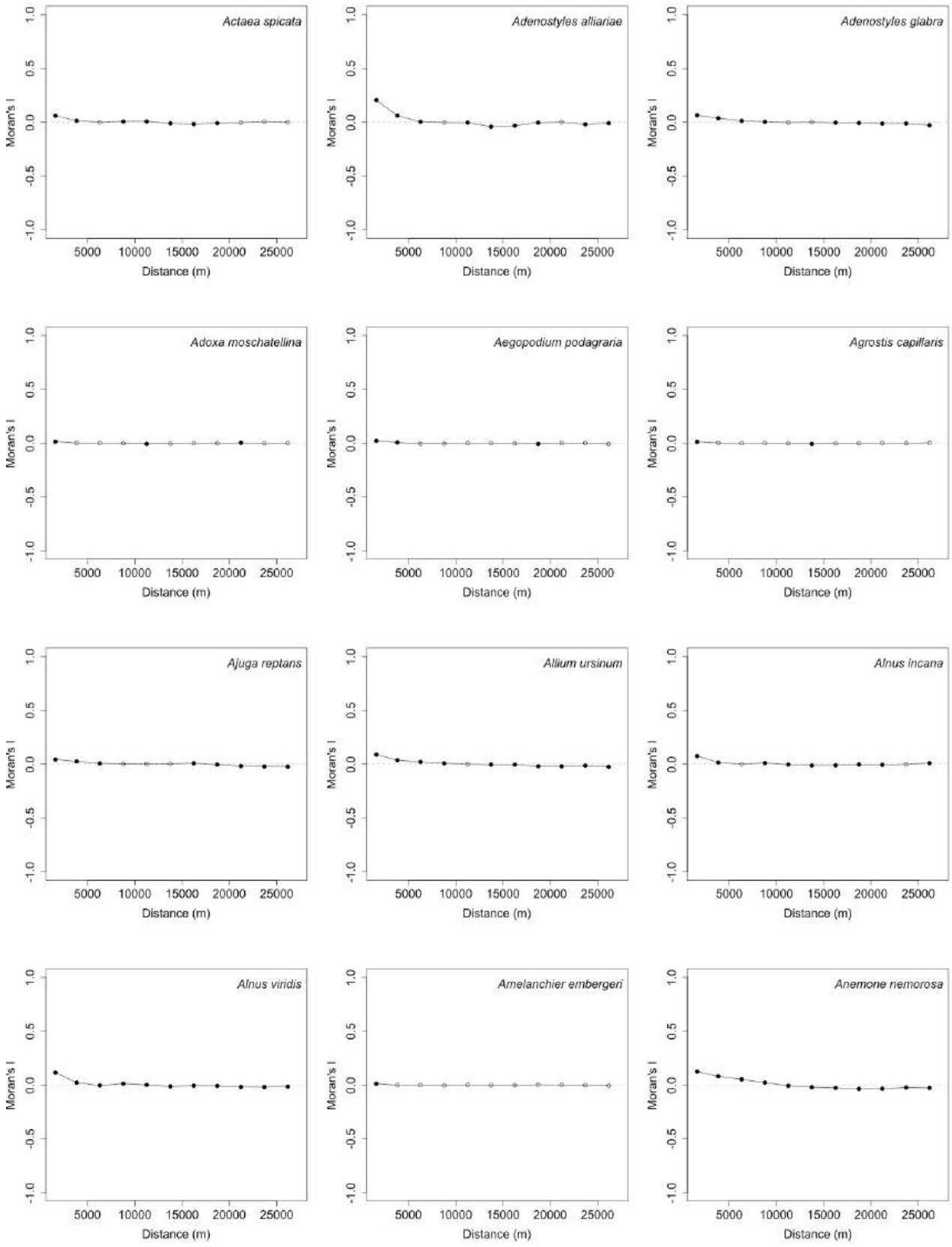
573 correlograms. All correlograms are globally significant at the α = 0.05 level since several individual values

574 are significant after Bonferroni correction. Filled symbols are significant values after Holm's correction for

575 multiple testing (α=0.05). Distances up to 2/3 of the maximum distance between two observations are

576 represented.

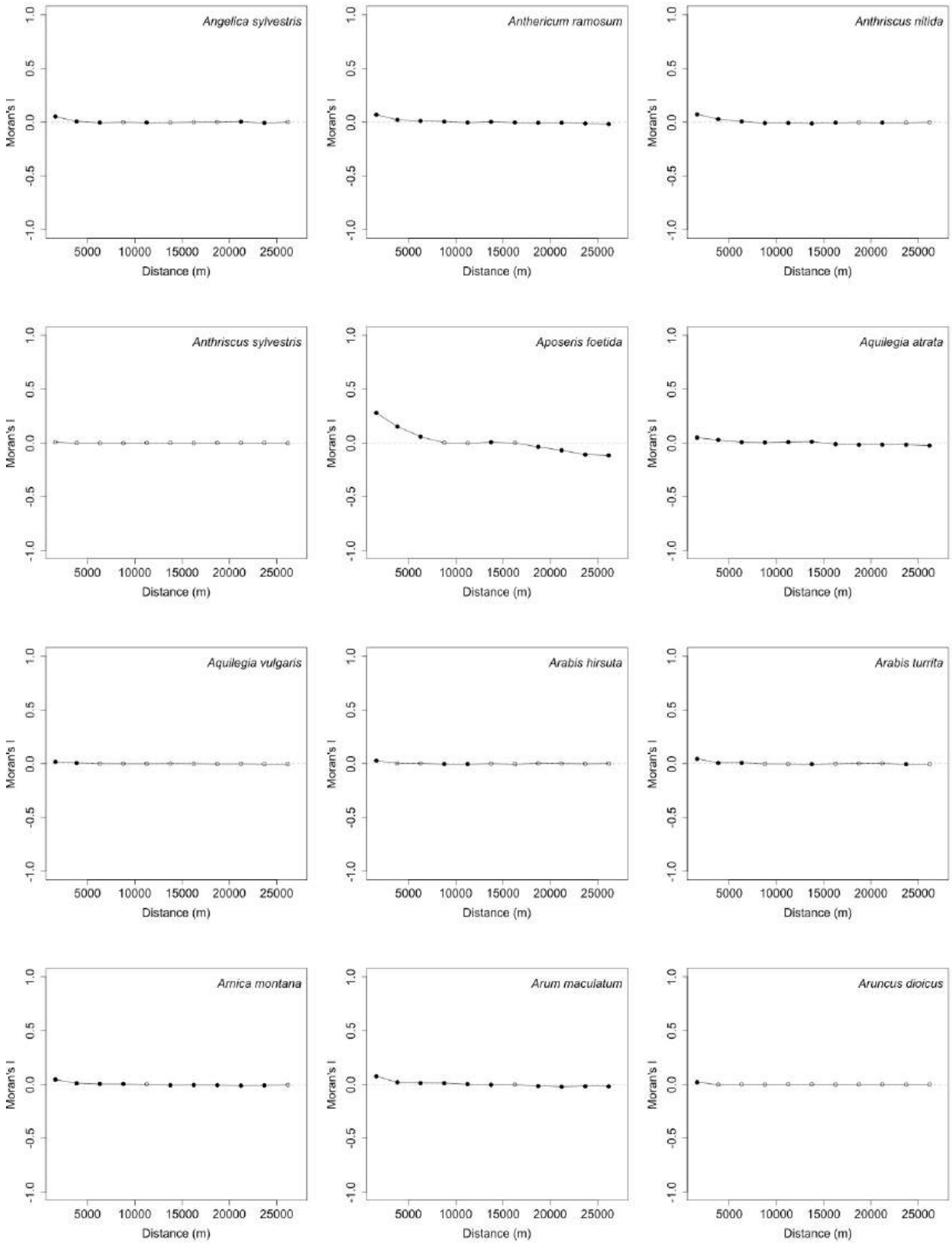
577



578

579 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

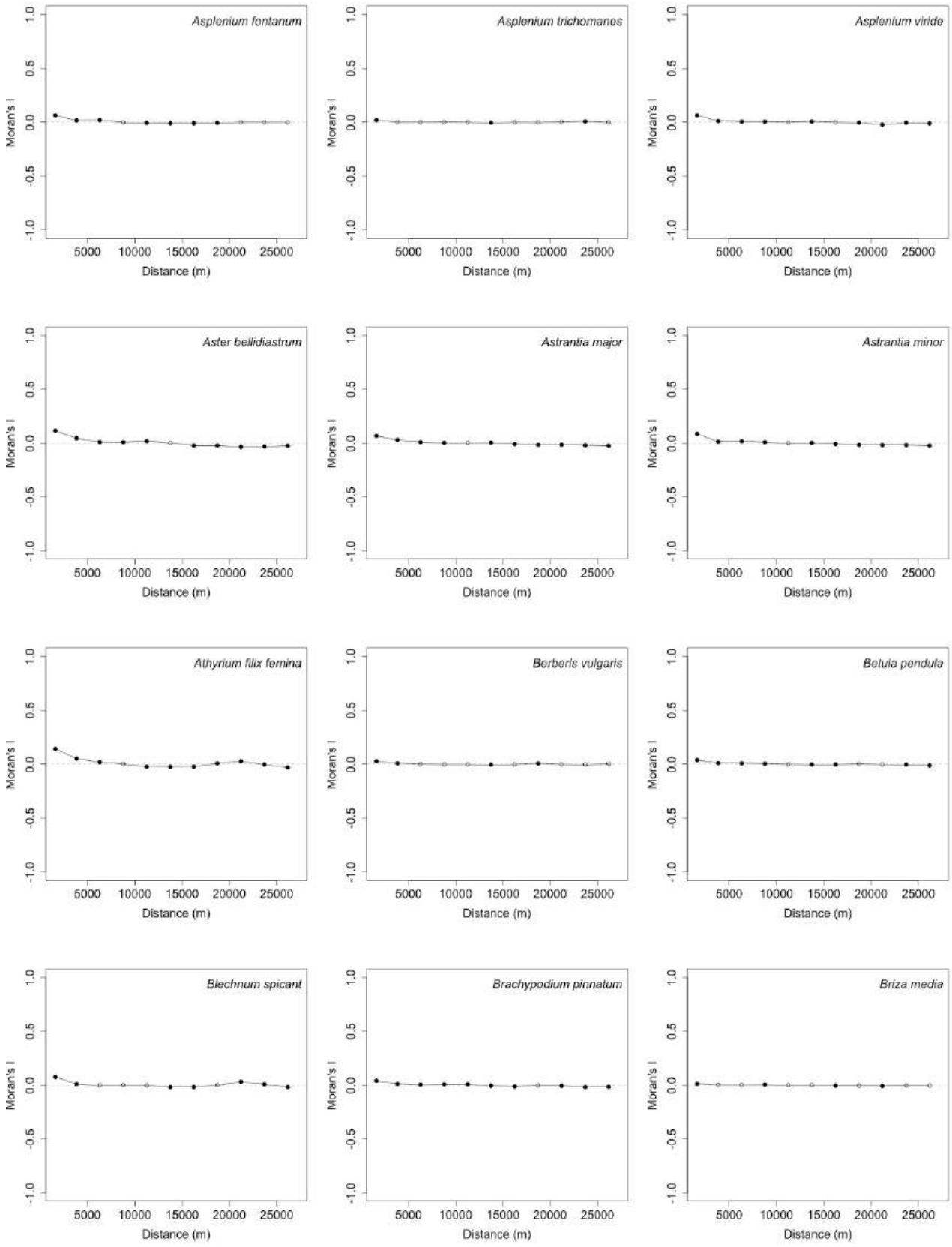
580 correlograms (cont.).



581

582 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

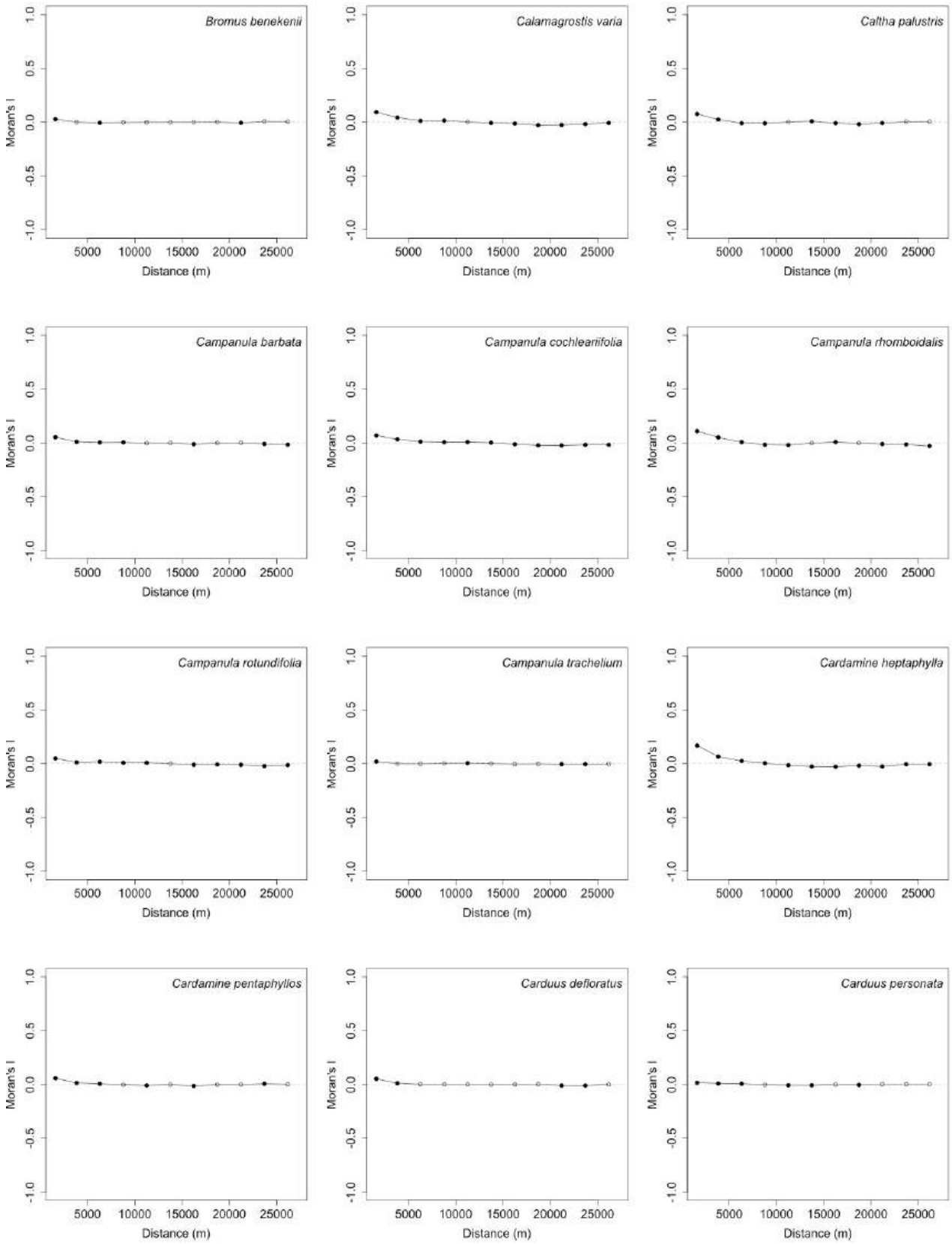
583 correlograms (cont.).



584

585 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

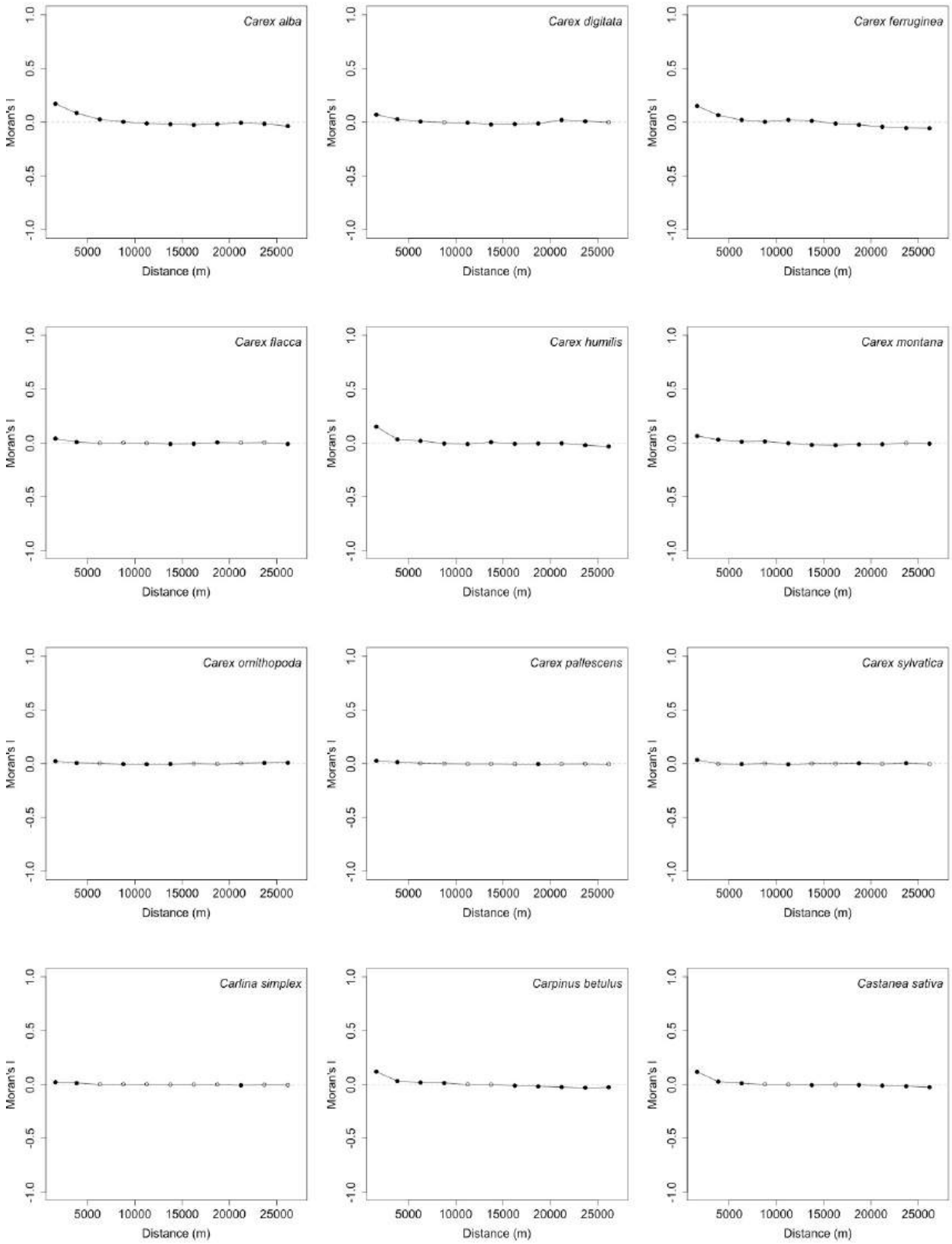
586 correlograms (cont.).



587

588 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

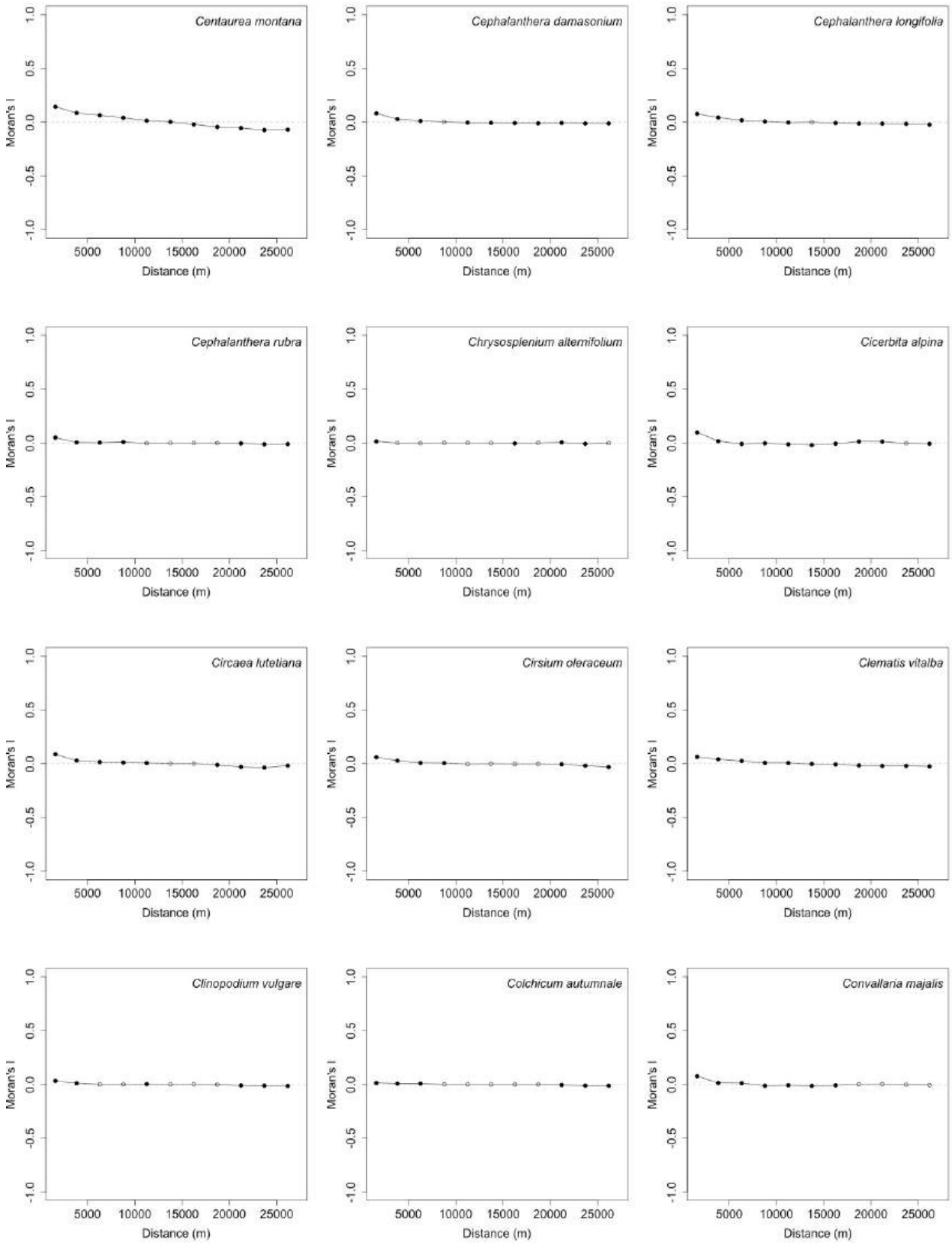
589 correlograms (cont.).



590

591 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

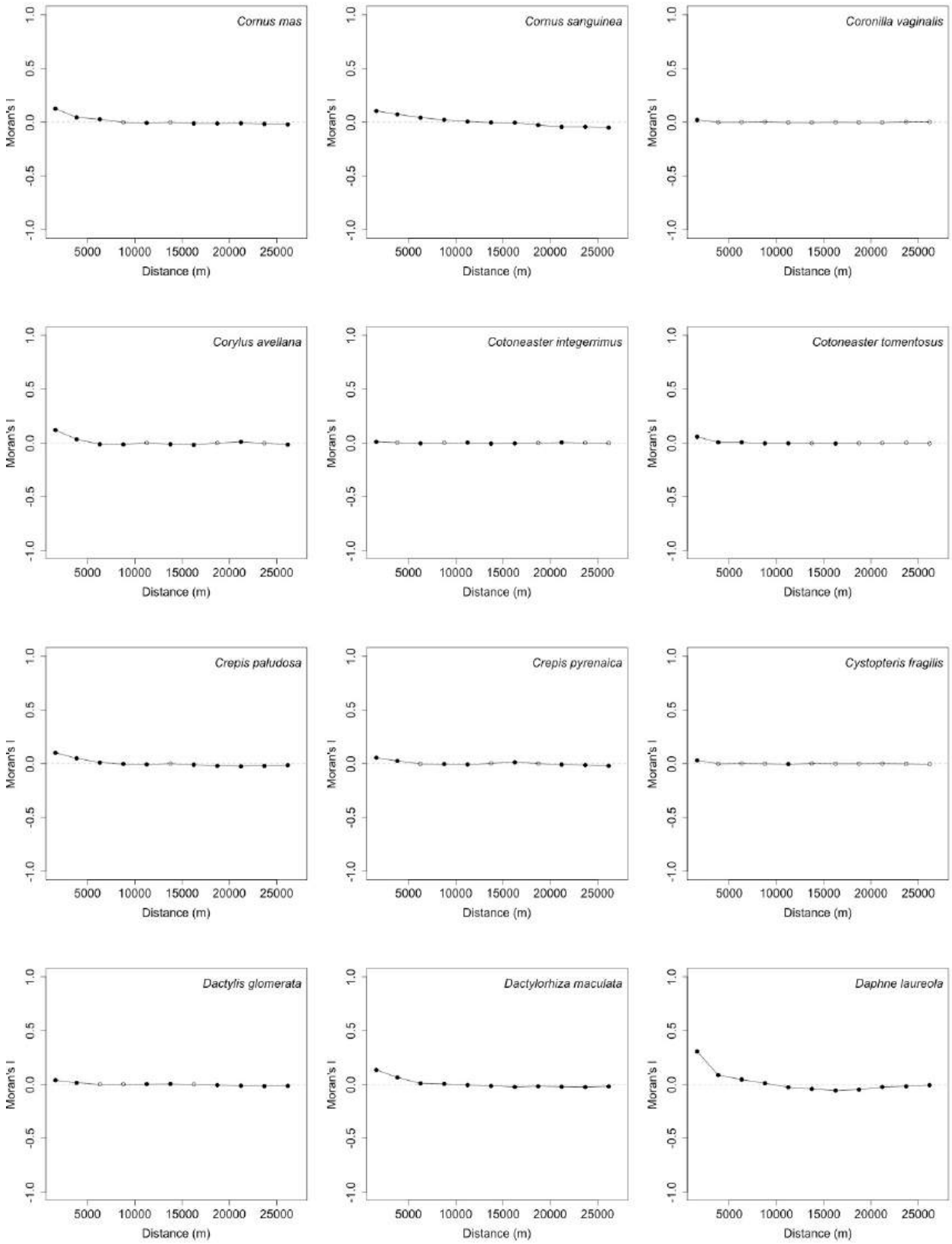
592 correlograms (cont.).



593

594 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

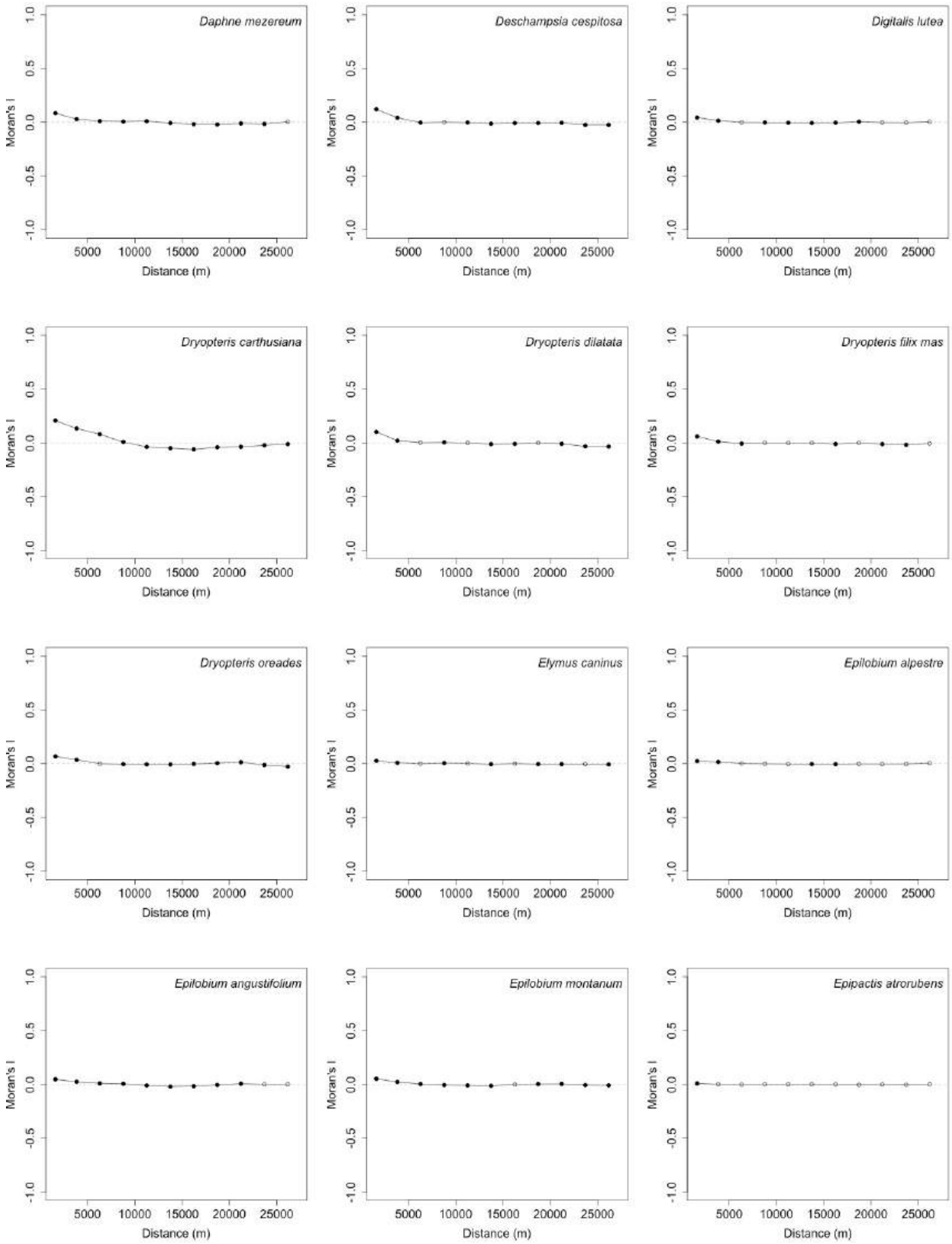
595 correlograms (cont.).



596

597 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

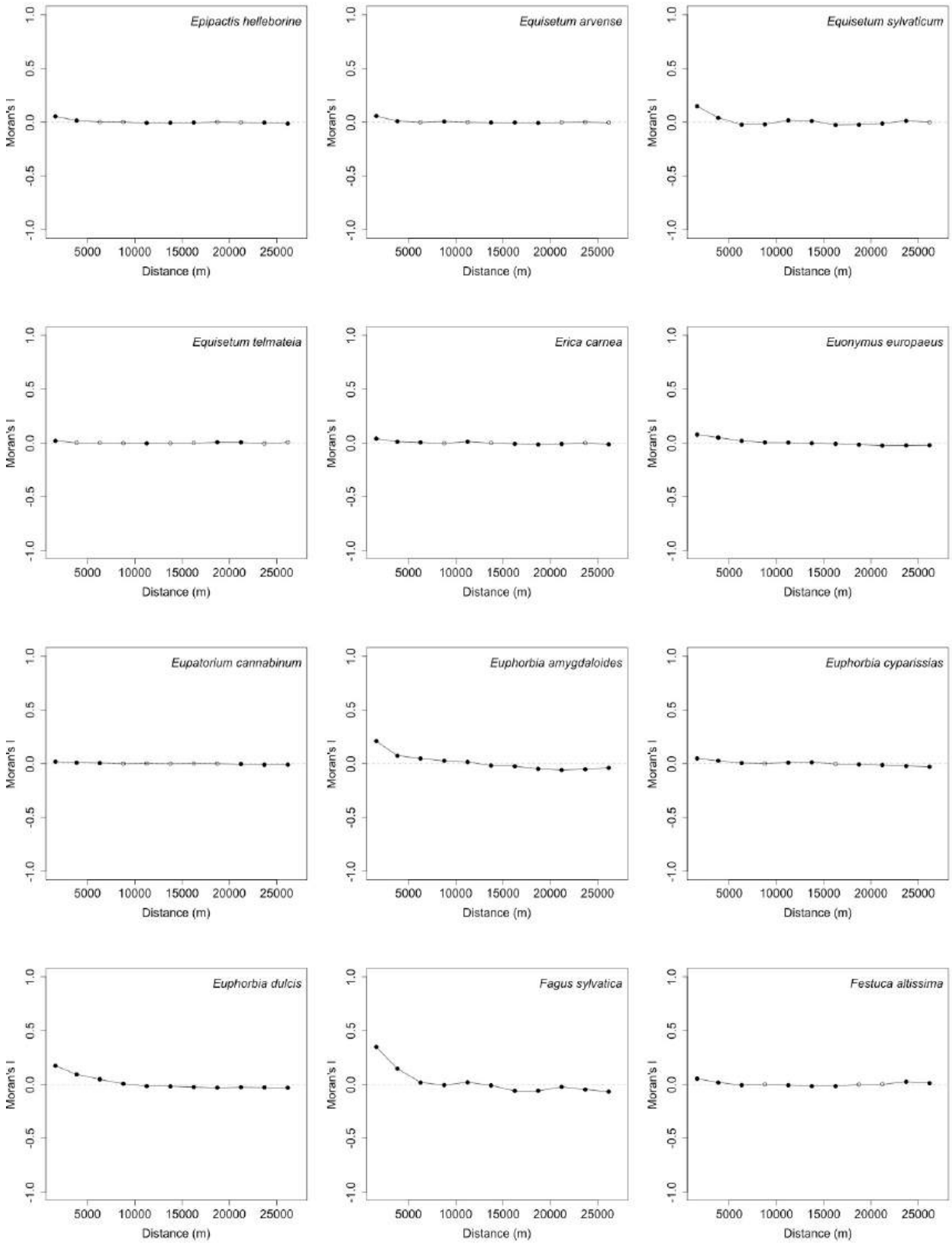
598 correlograms (cont.).



599

600 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

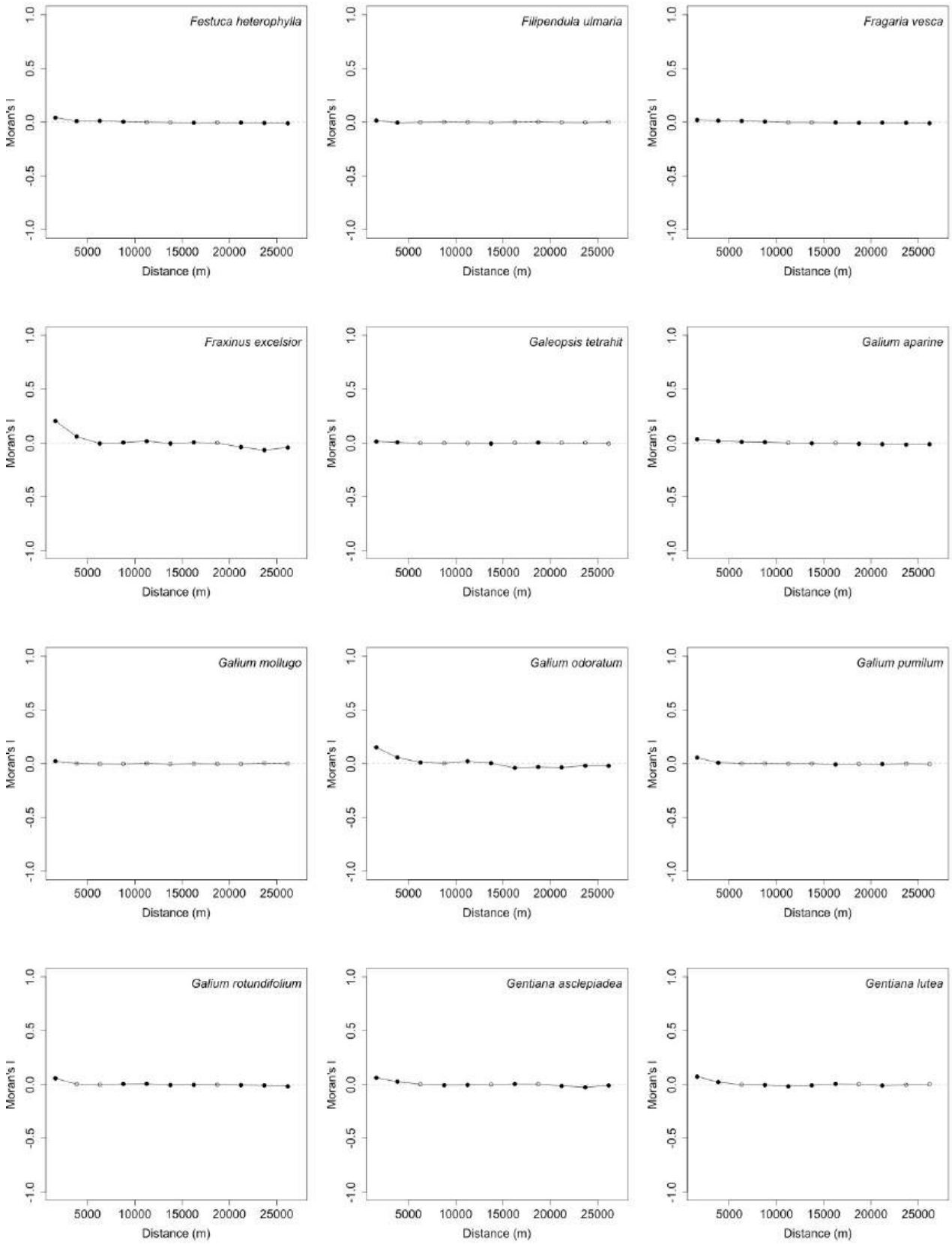
601 correlograms (cont.).



602

603 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

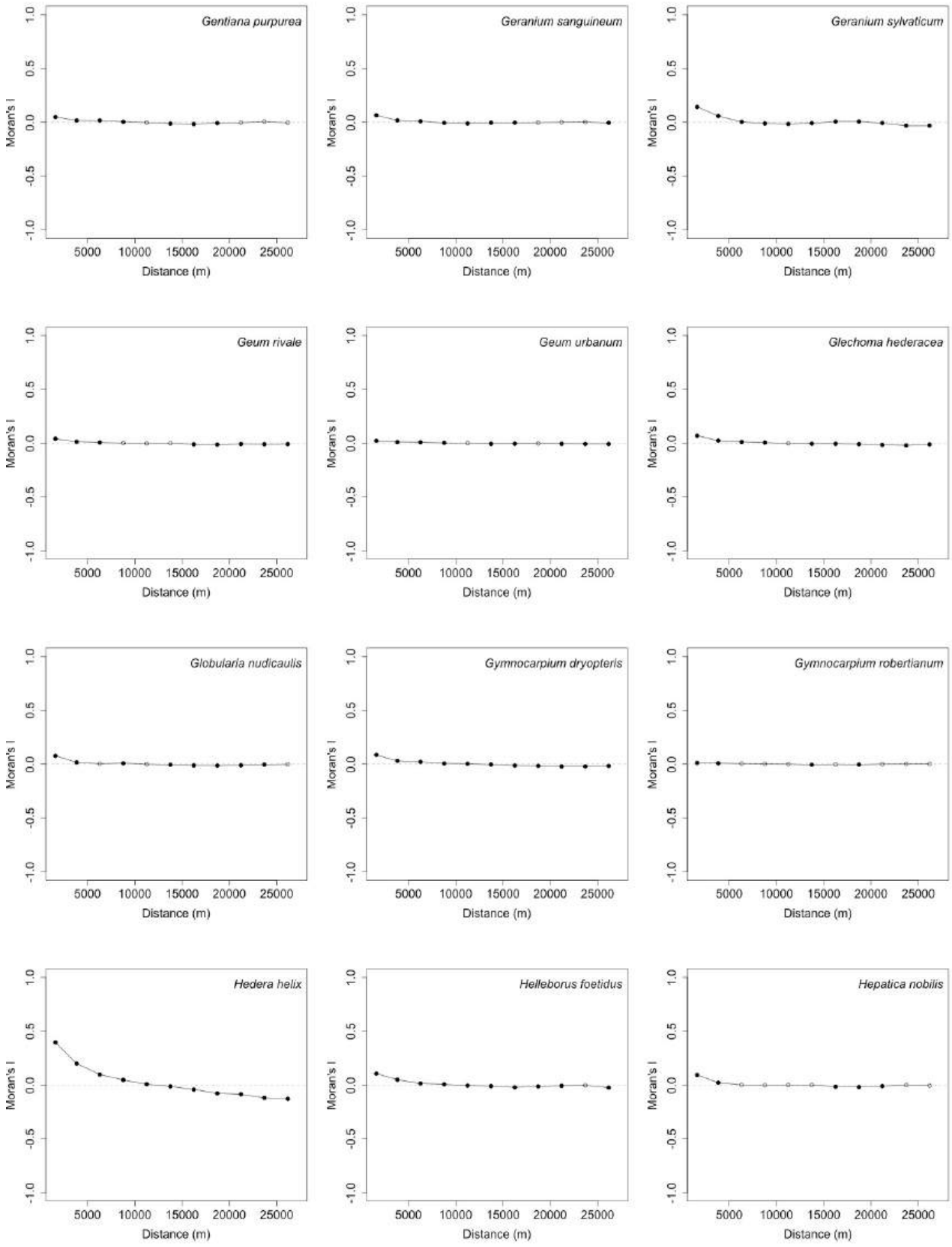
604 correlograms (cont.).



605

606 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

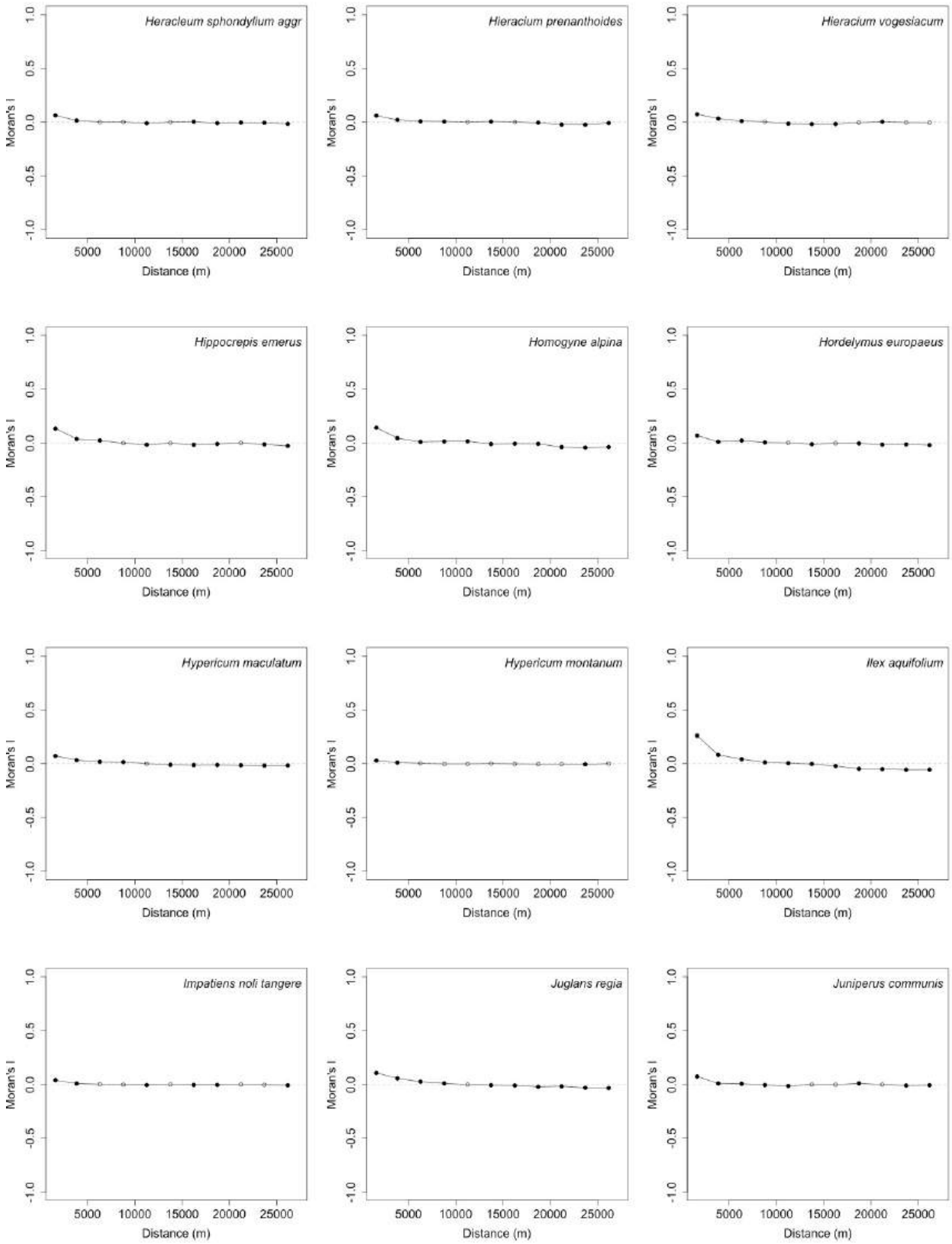
607 correlograms (cont.).



608

609 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

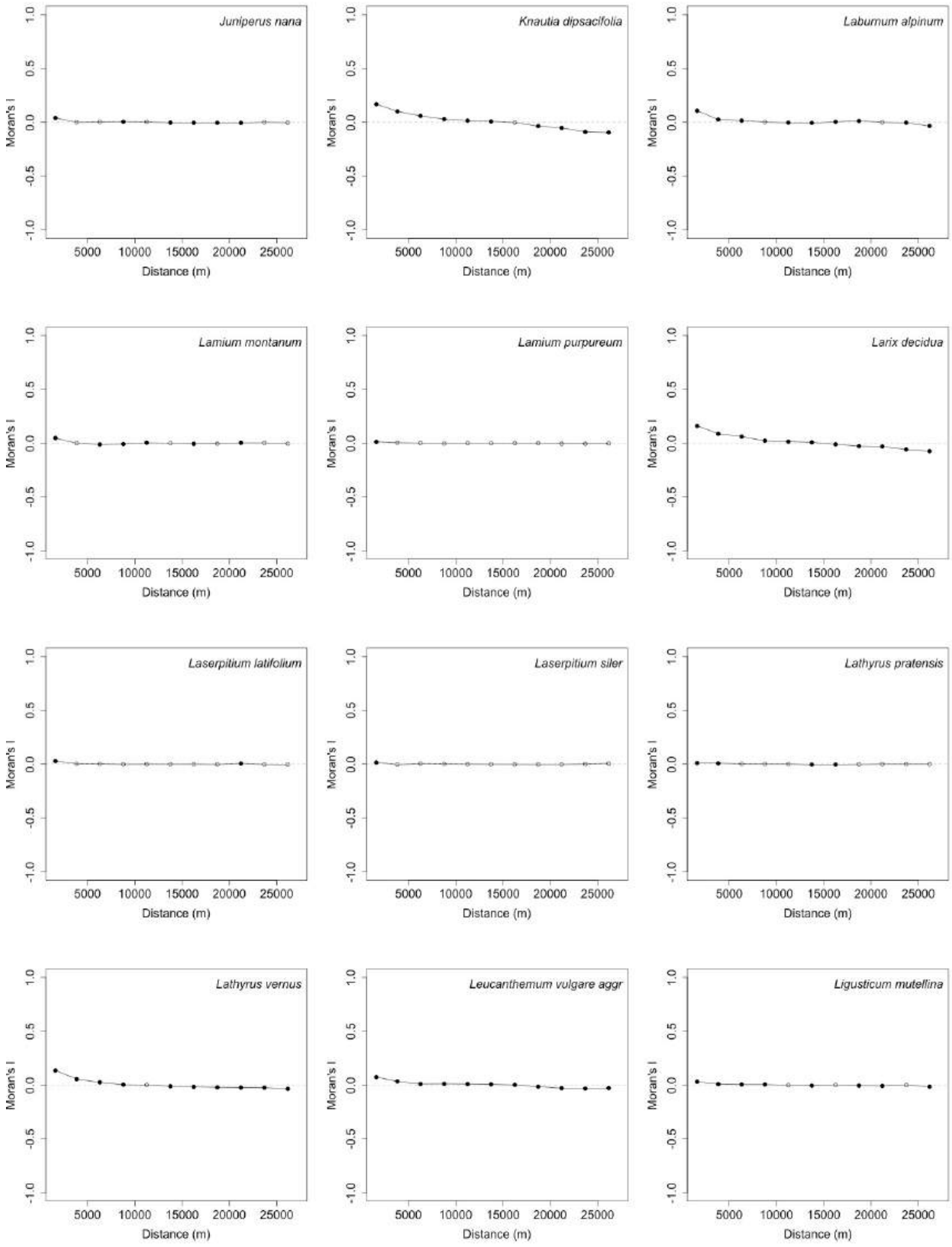
610 correlograms (cont.).



611

612 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

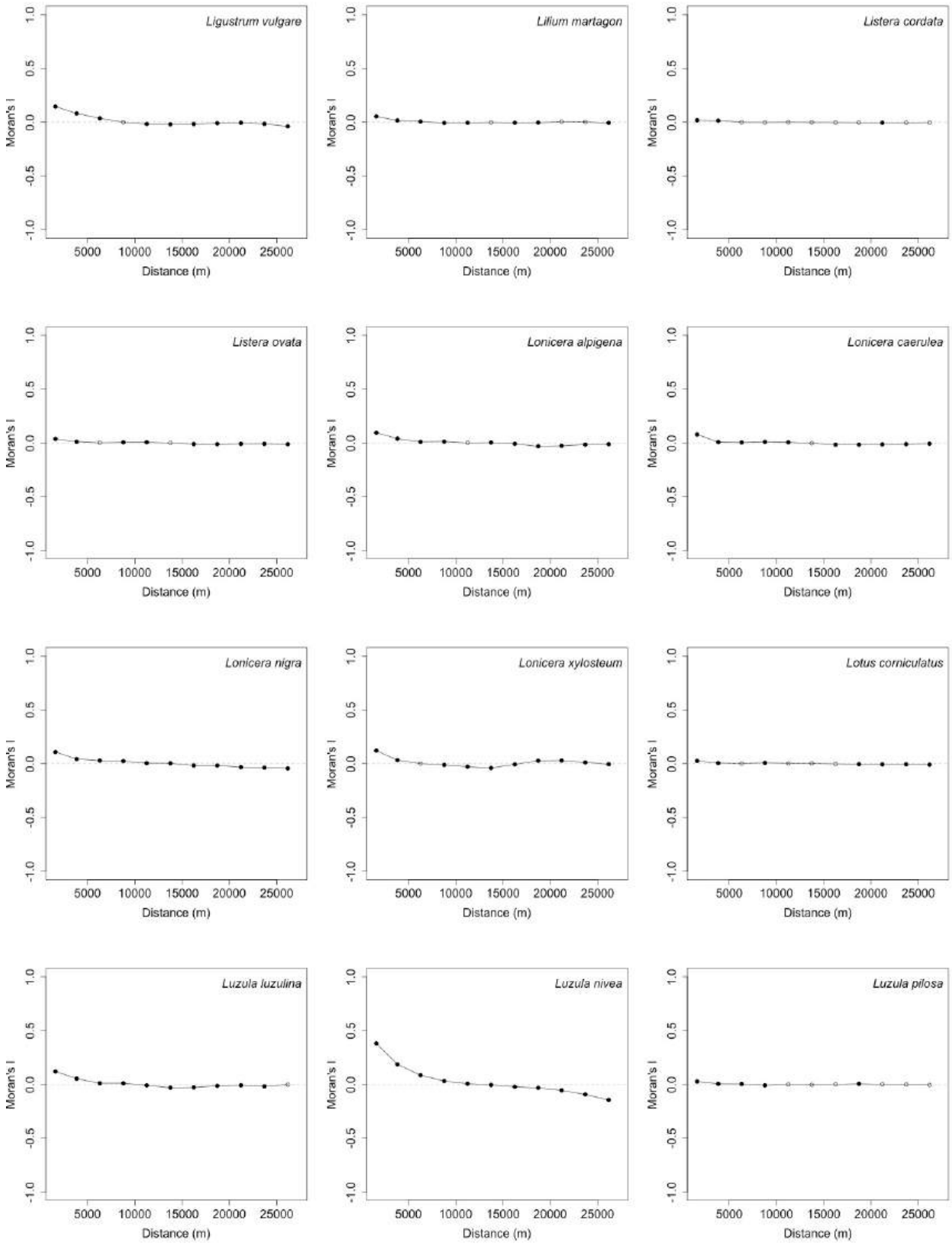
613 correlograms (cont.).



614

615 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

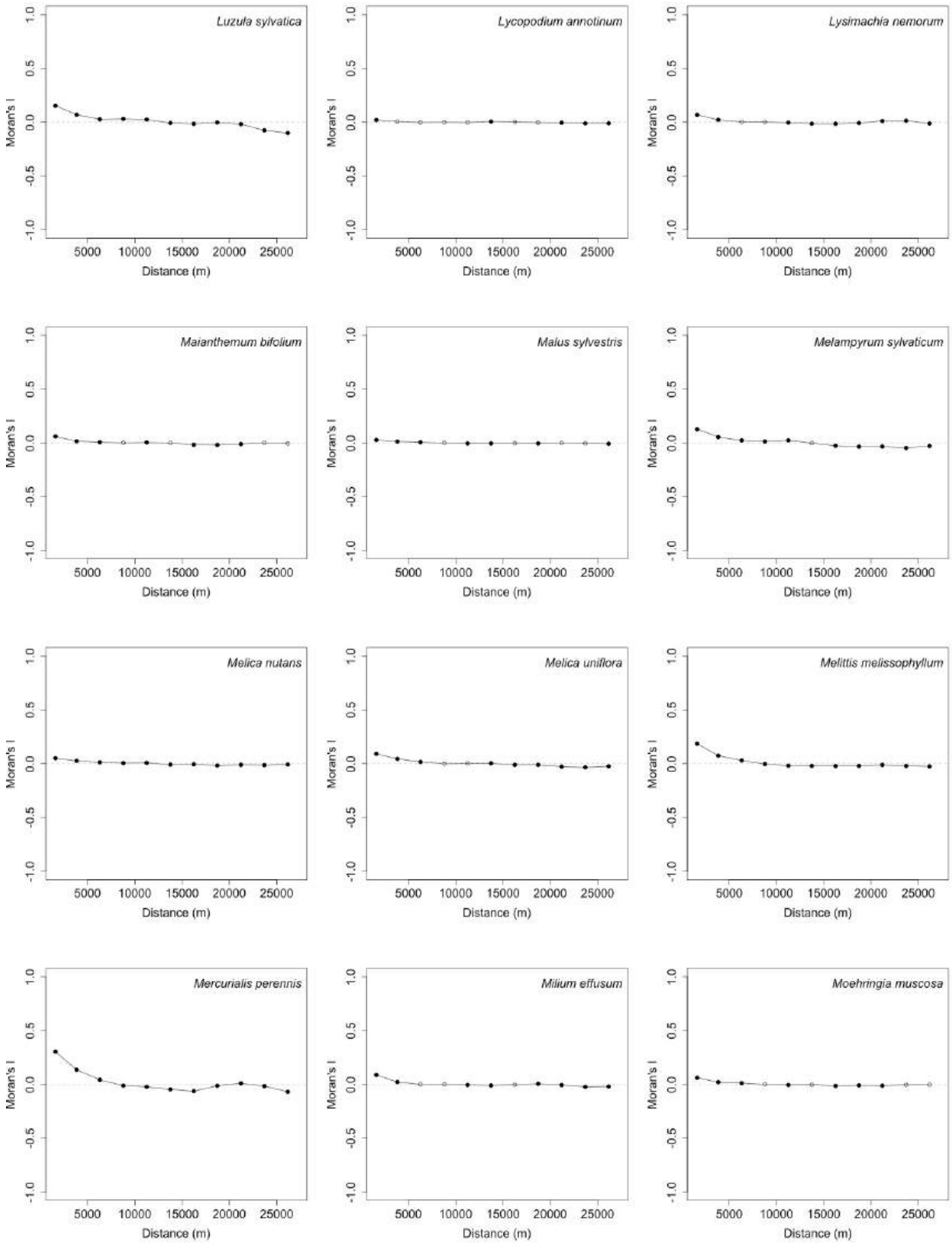
616 correlograms (cont.).



617

618 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

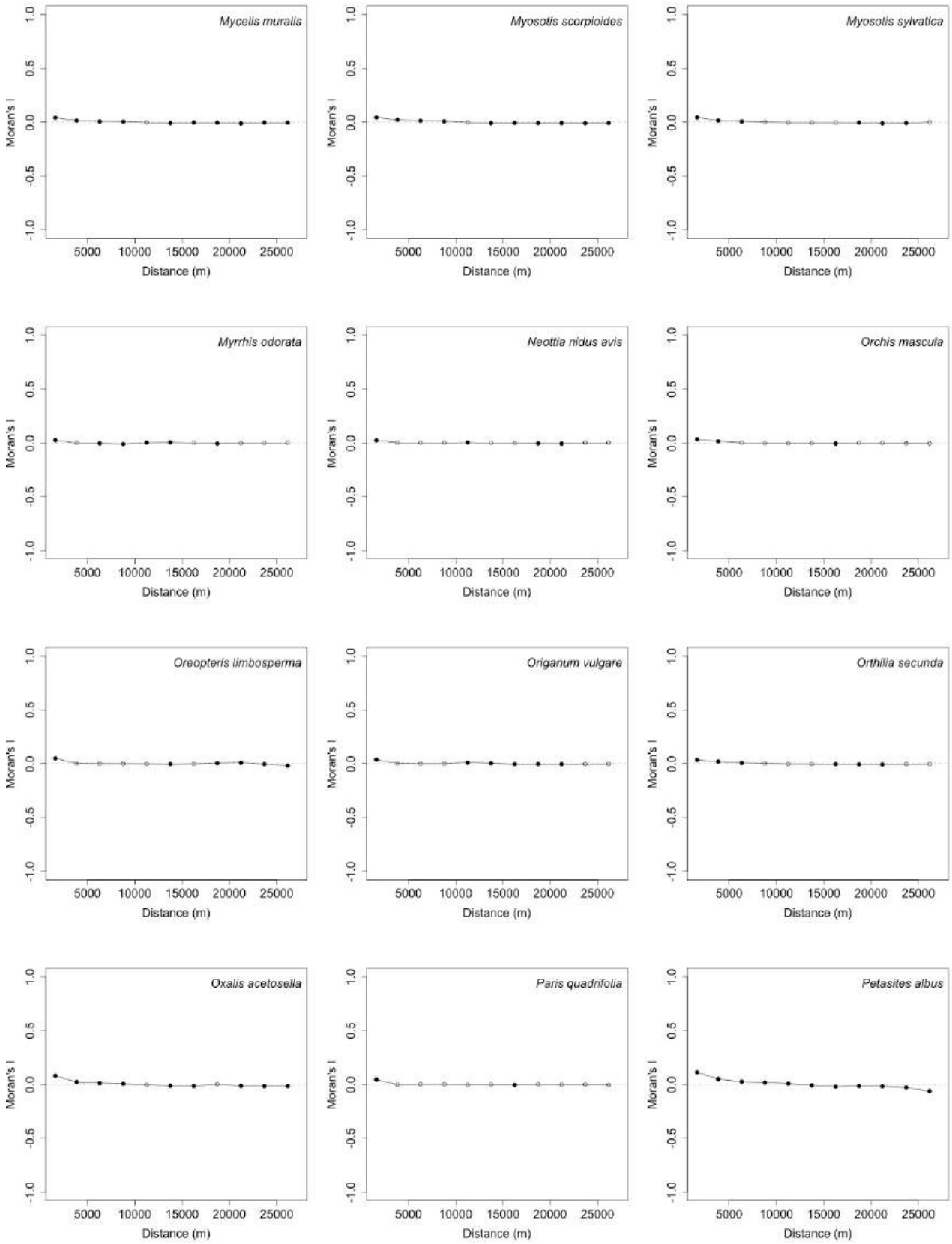
619 correlograms (cont.).



620

621 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

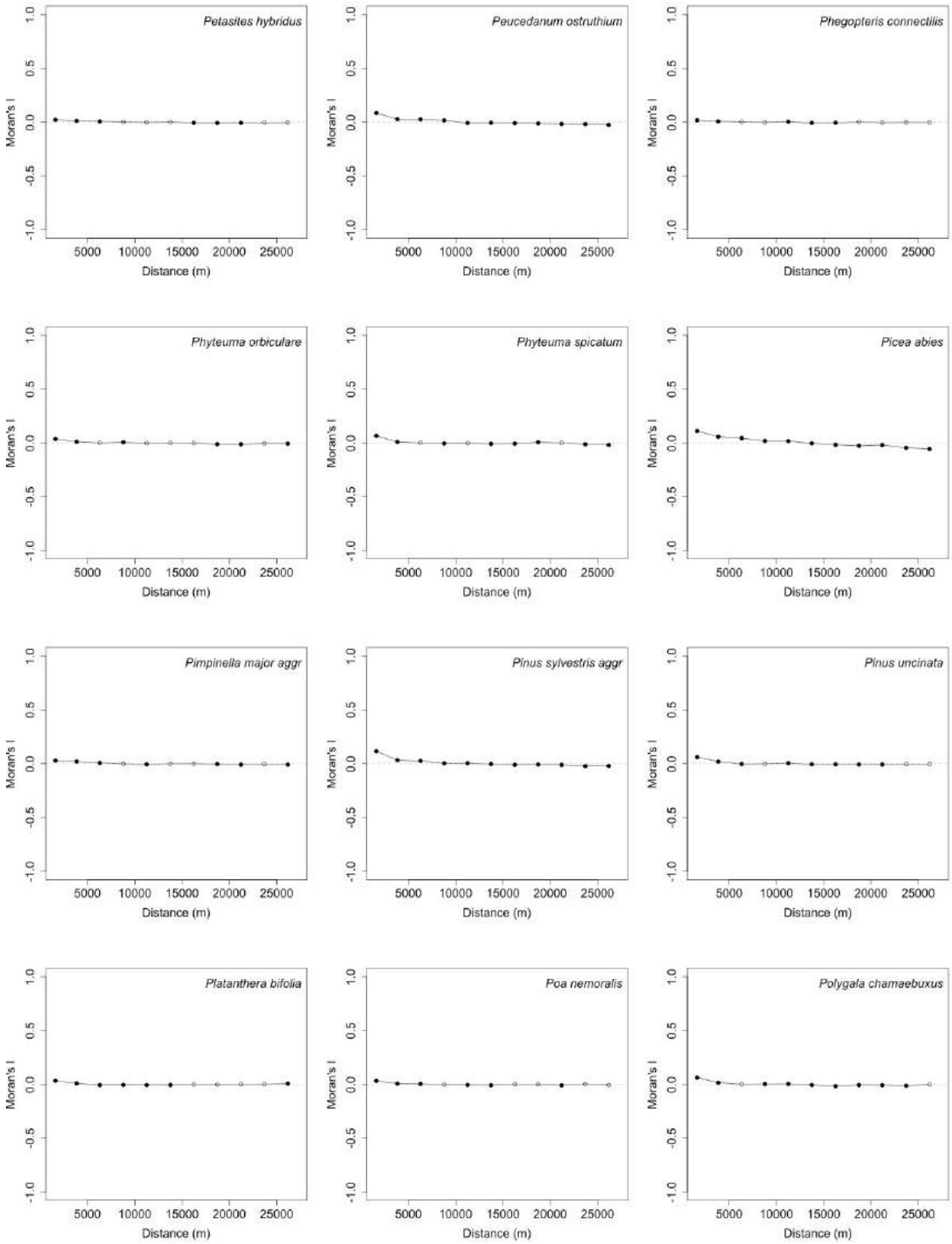
622 correlograms (cont.).



623

624 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

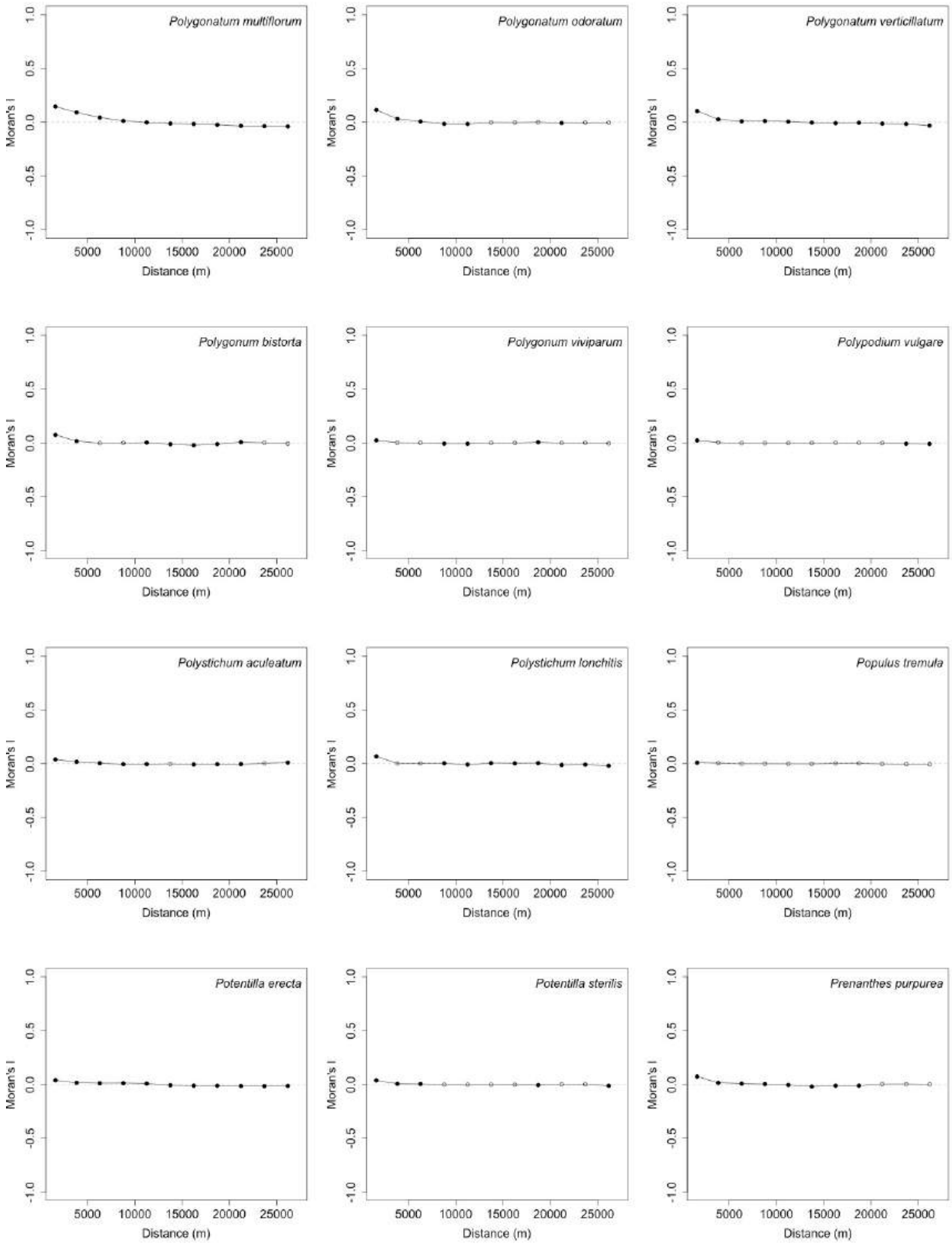
625 correlograms (cont.).



626

627 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

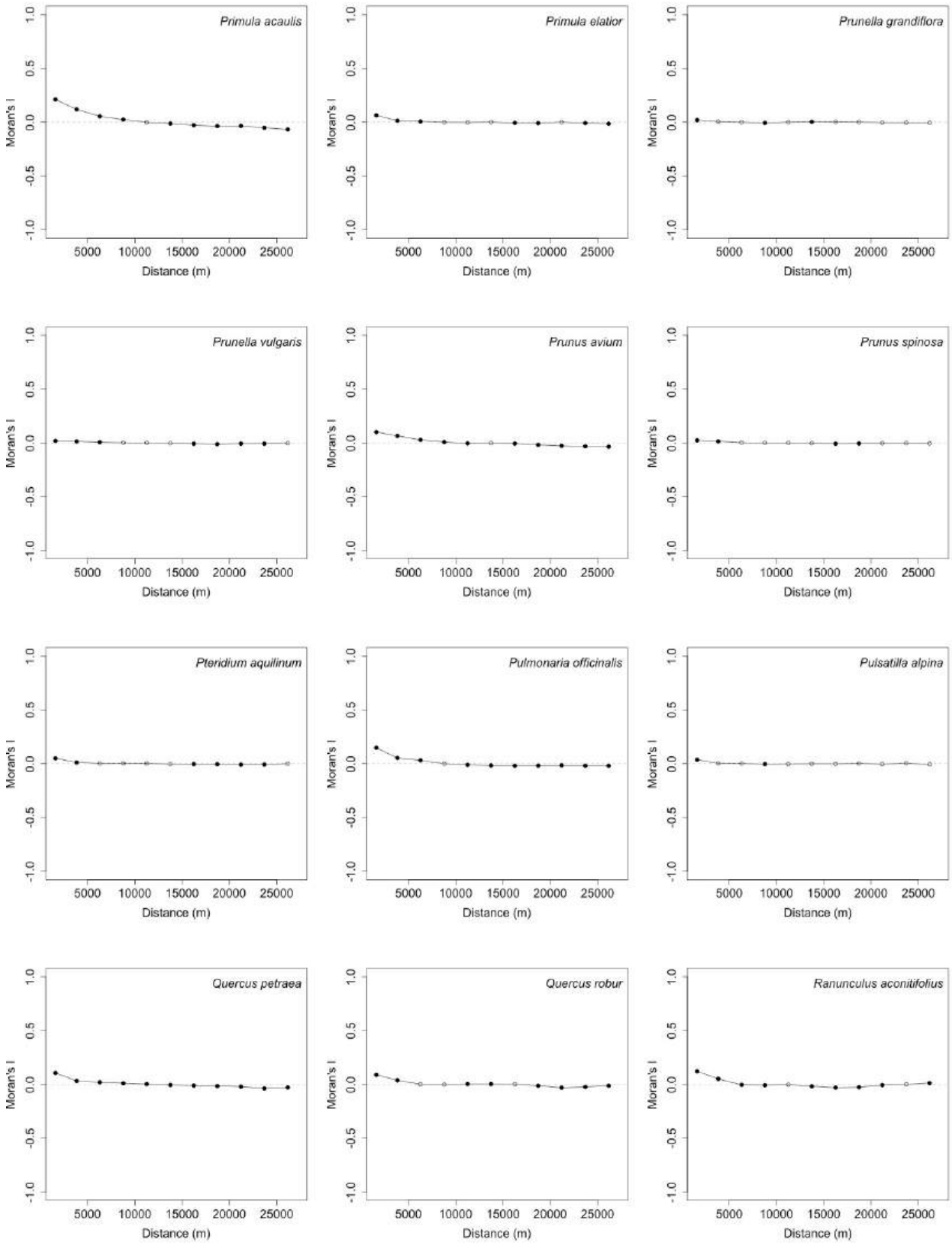
628 correlograms (cont.).



629

630 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

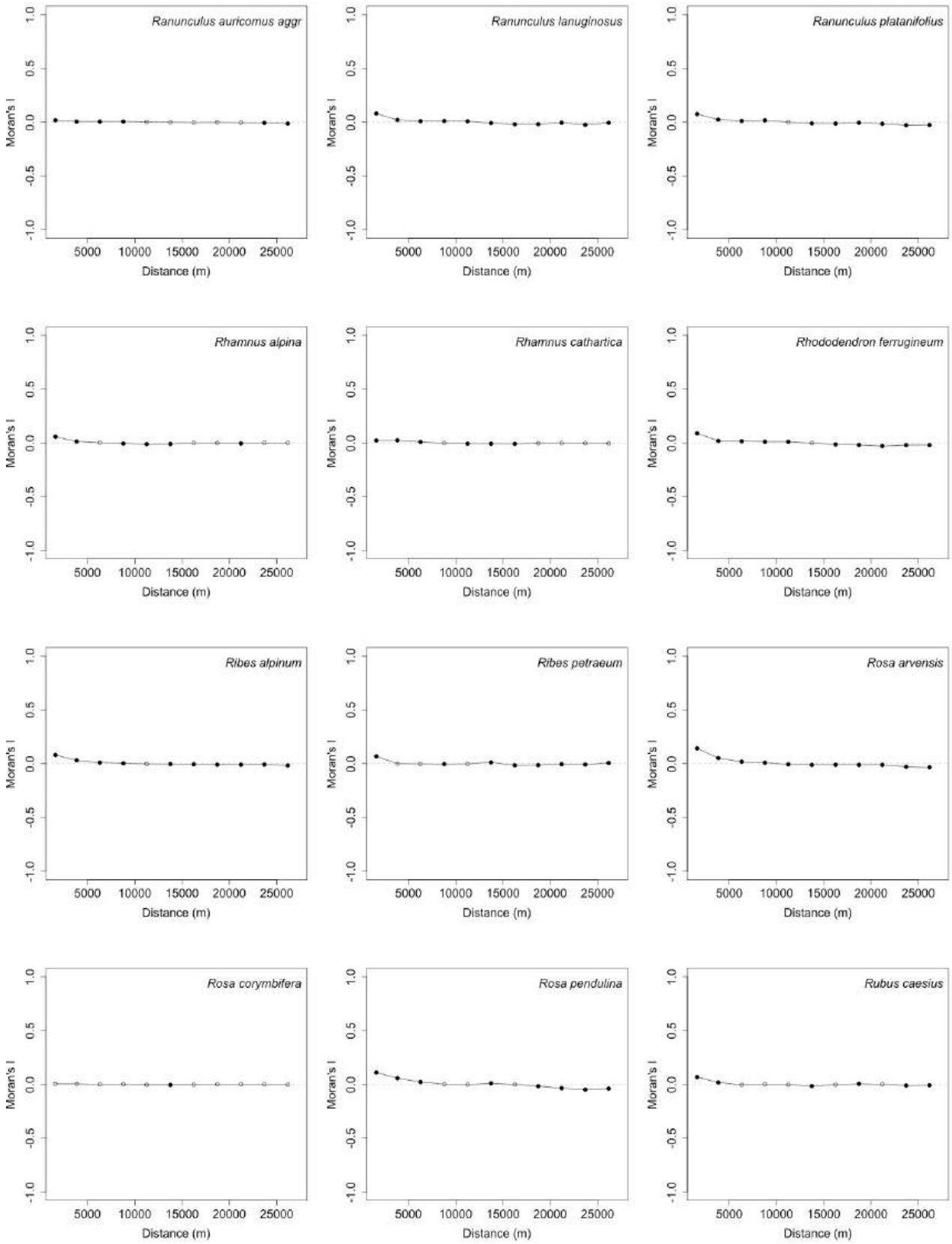
631 correlograms (cont.).



632

633 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

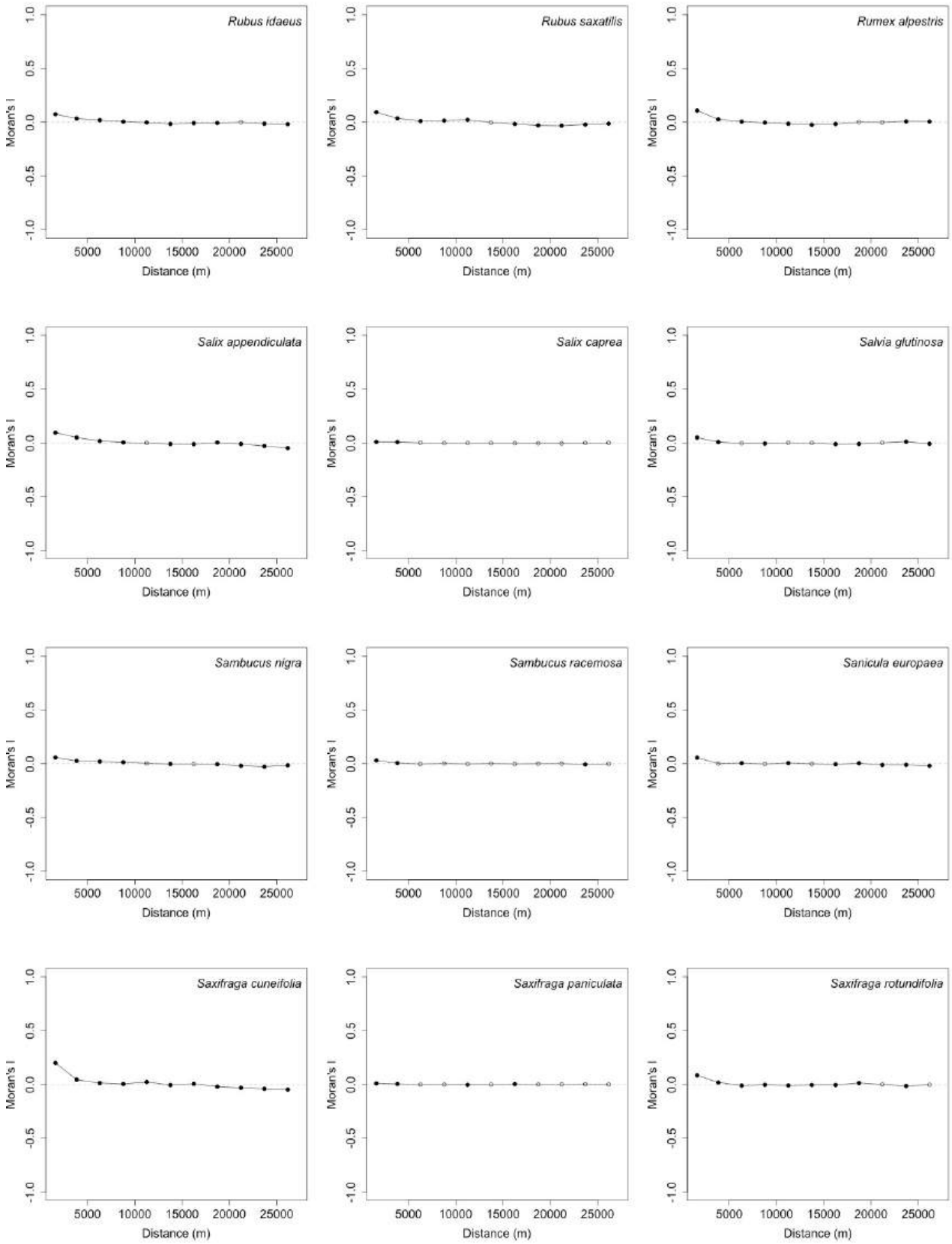
634 correlograms (cont.).



635

636 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

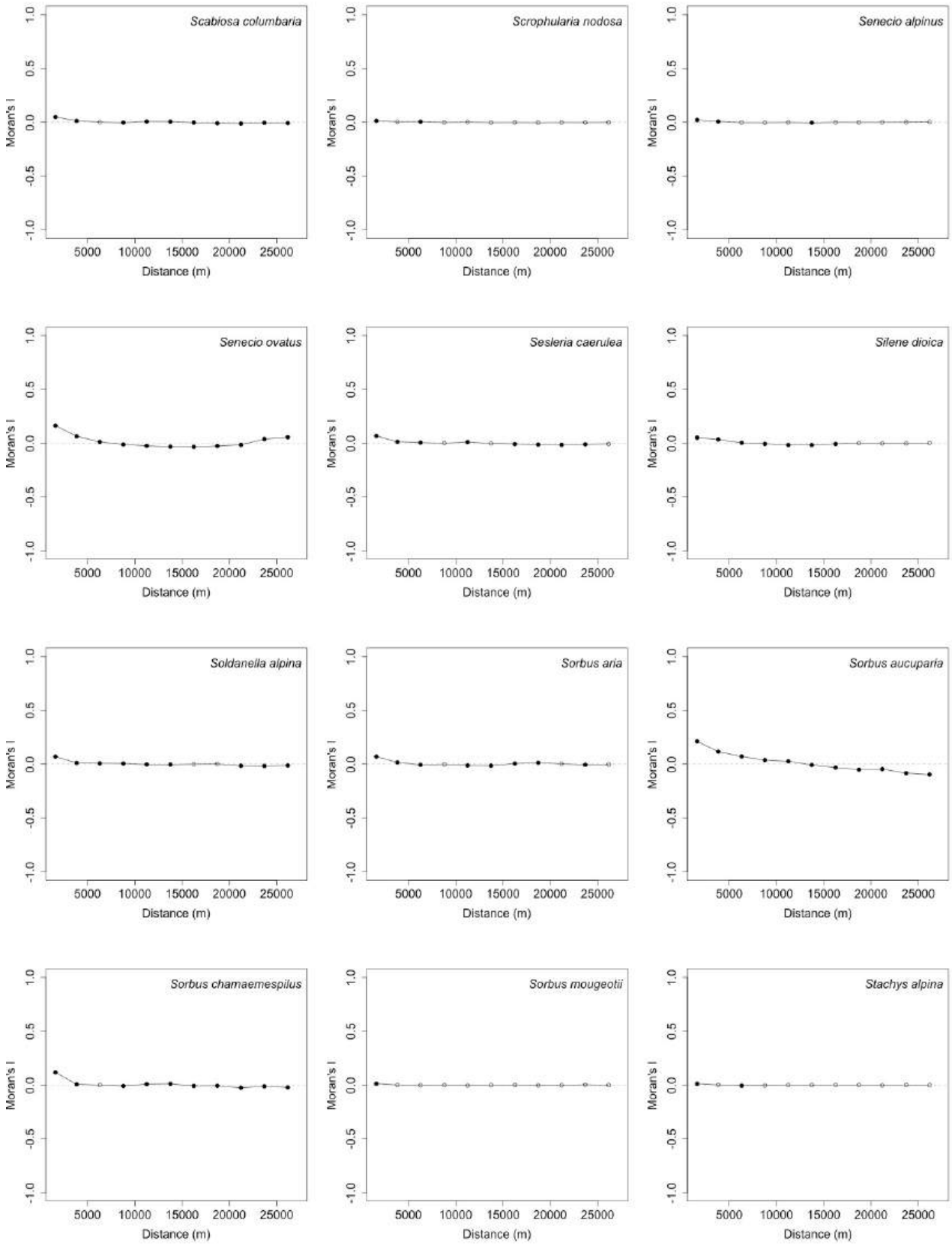
637 correlograms (cont.).



638

639 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

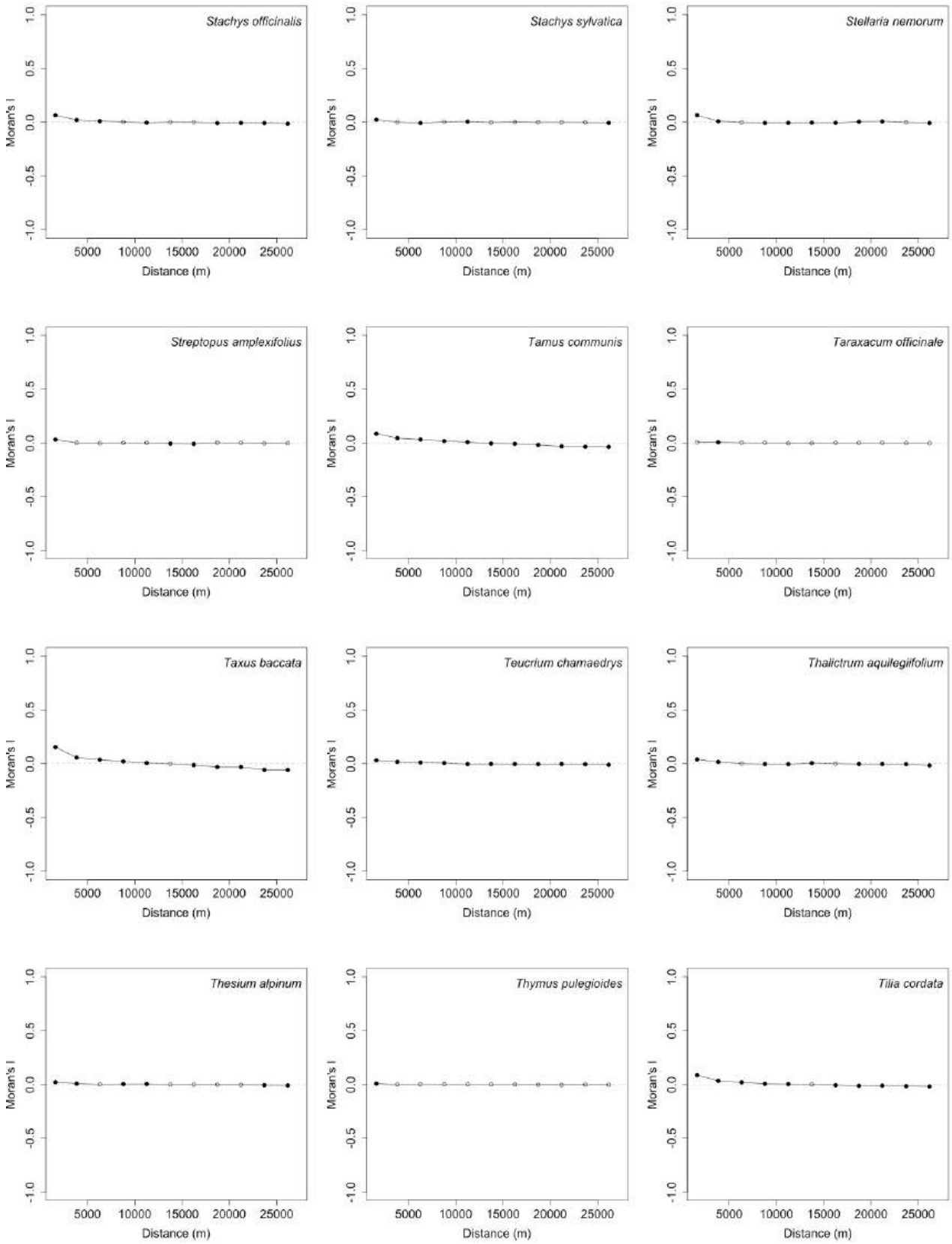
640 correlograms (cont.).



641

642 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

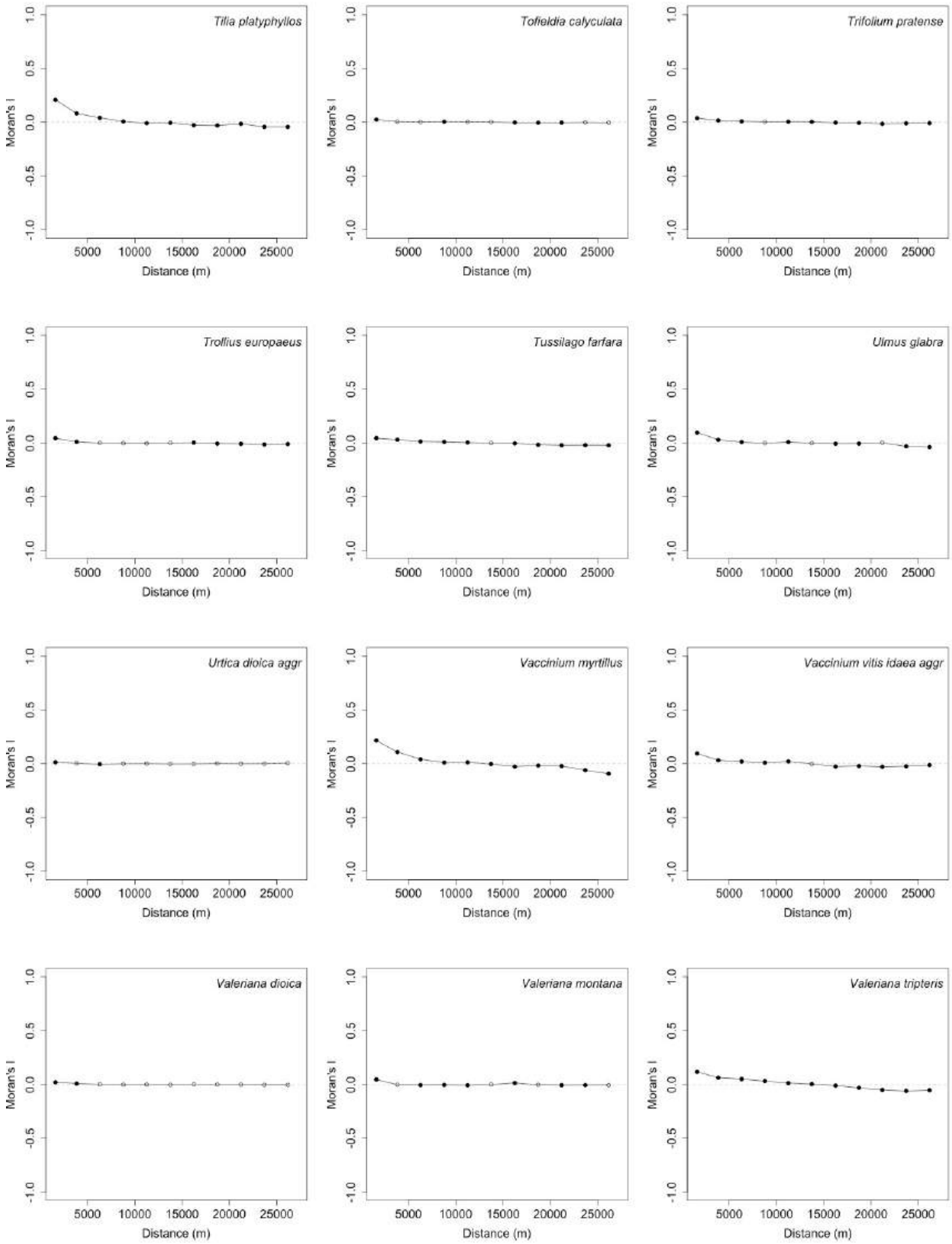
643 correlograms (cont.).



644

645 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

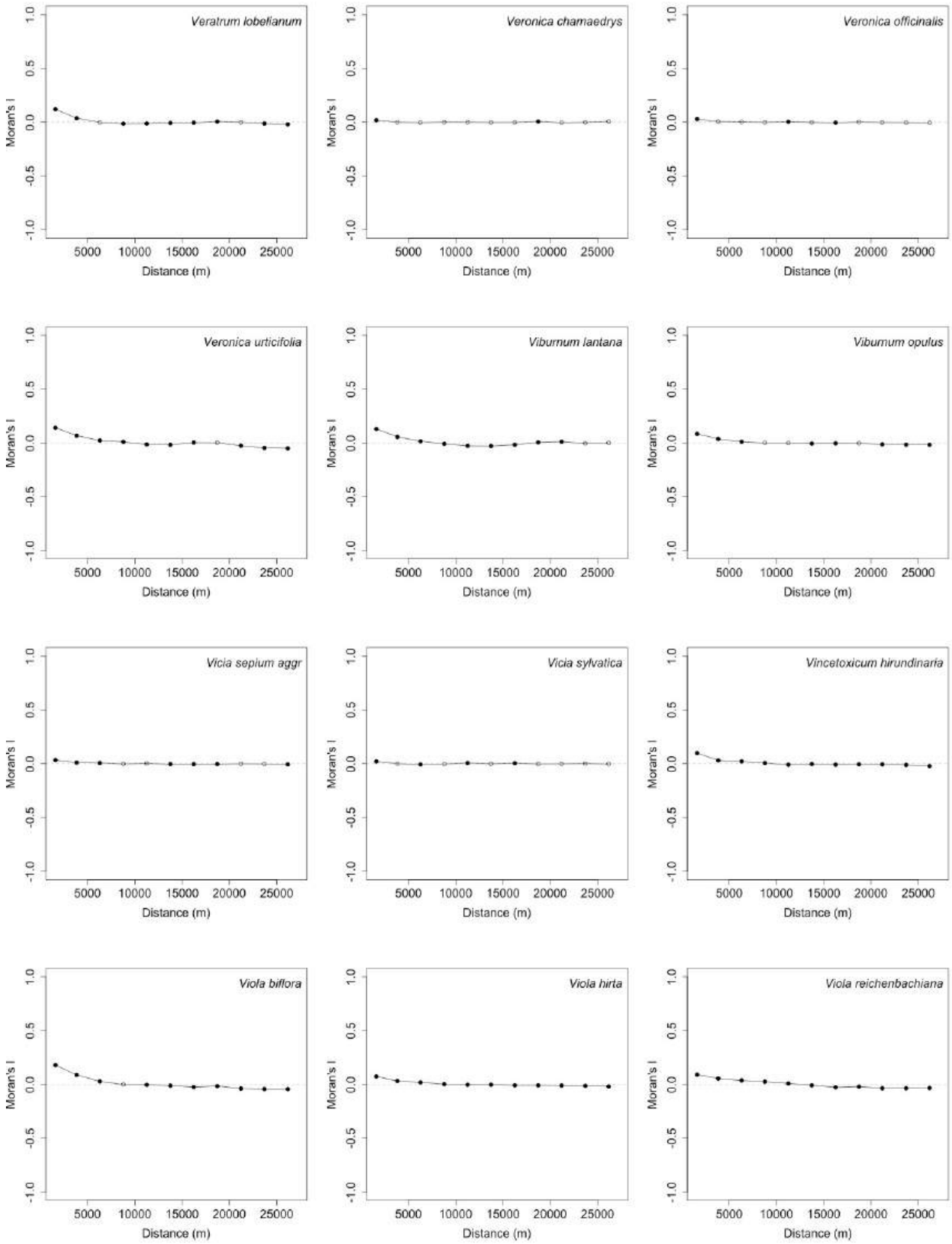
646 correlograms (cont.).



647

648 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

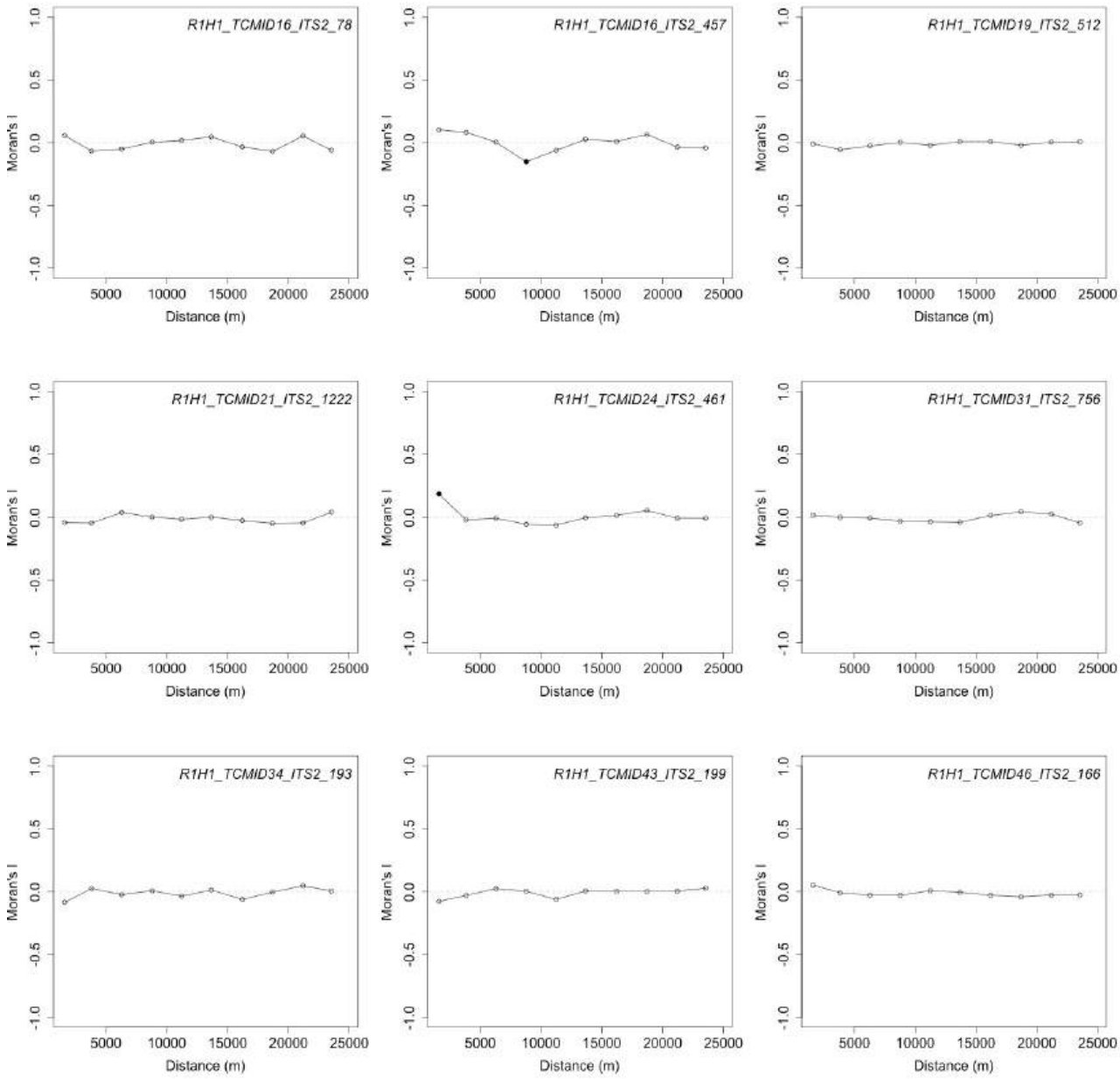
649 correlograms (cont.).



650

651 **Figure S5** Spatial autocorrelation of each species of the *Forest* group based on Moran's *I* spatial

652 correlograms (cont.).



653

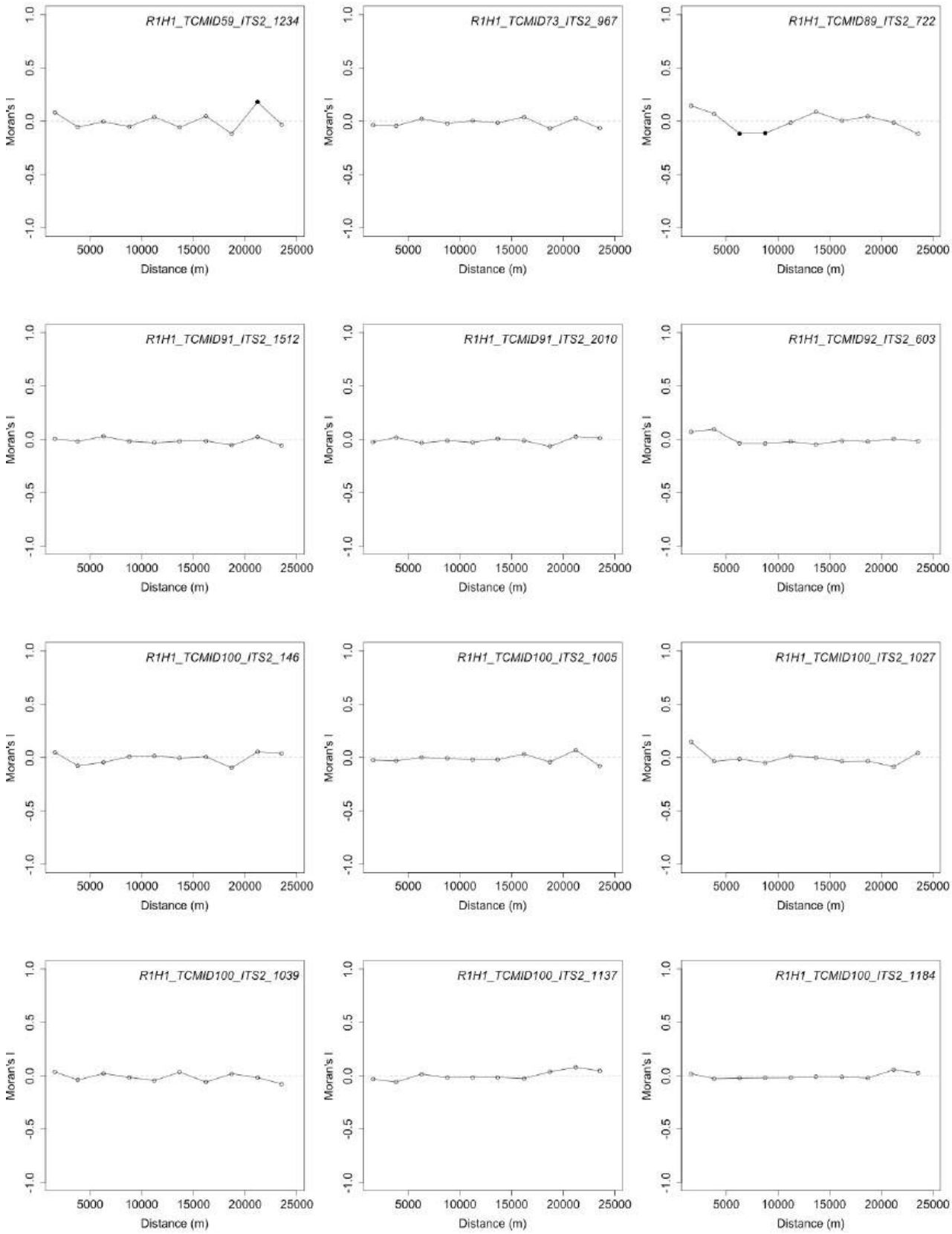
654 **Figure S6** Spatial autocorrelation of each species of the *Fungi* group based on Moran's *I* spatial

655 correlograms. All correlograms are globally significant at the α = 0.05 level since several individual values

656 are significant after Bonferroni correction. Filled symbols are significant values after Holm's correction for

657 multiple testing (α=0.05). Distances up to 2/3 of the maximum distance between two observations are

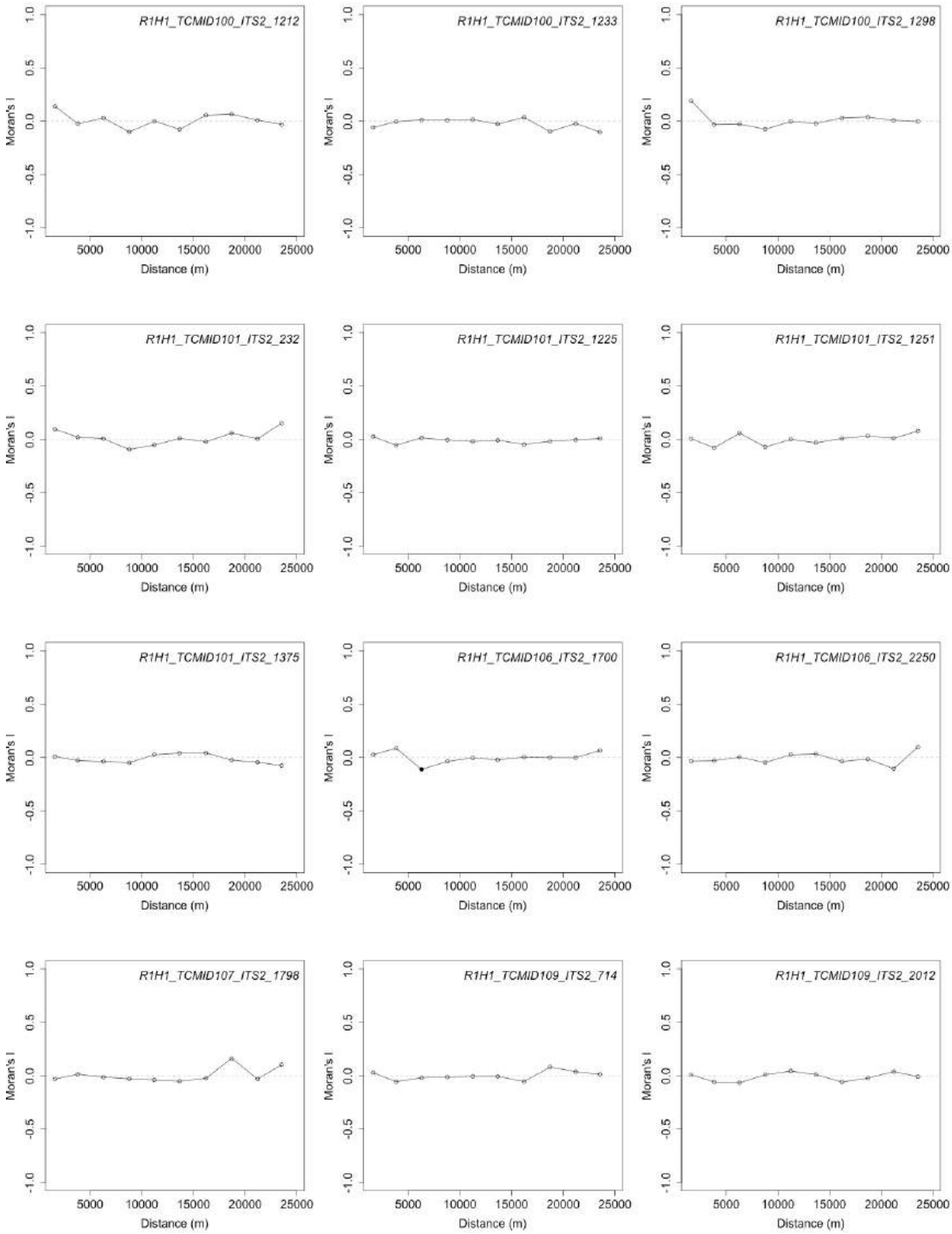
658 represented.



659

660 **Figure S6** Spatial autocorrelation of each species of the *Fungi* group based on Moran's *I* spatial

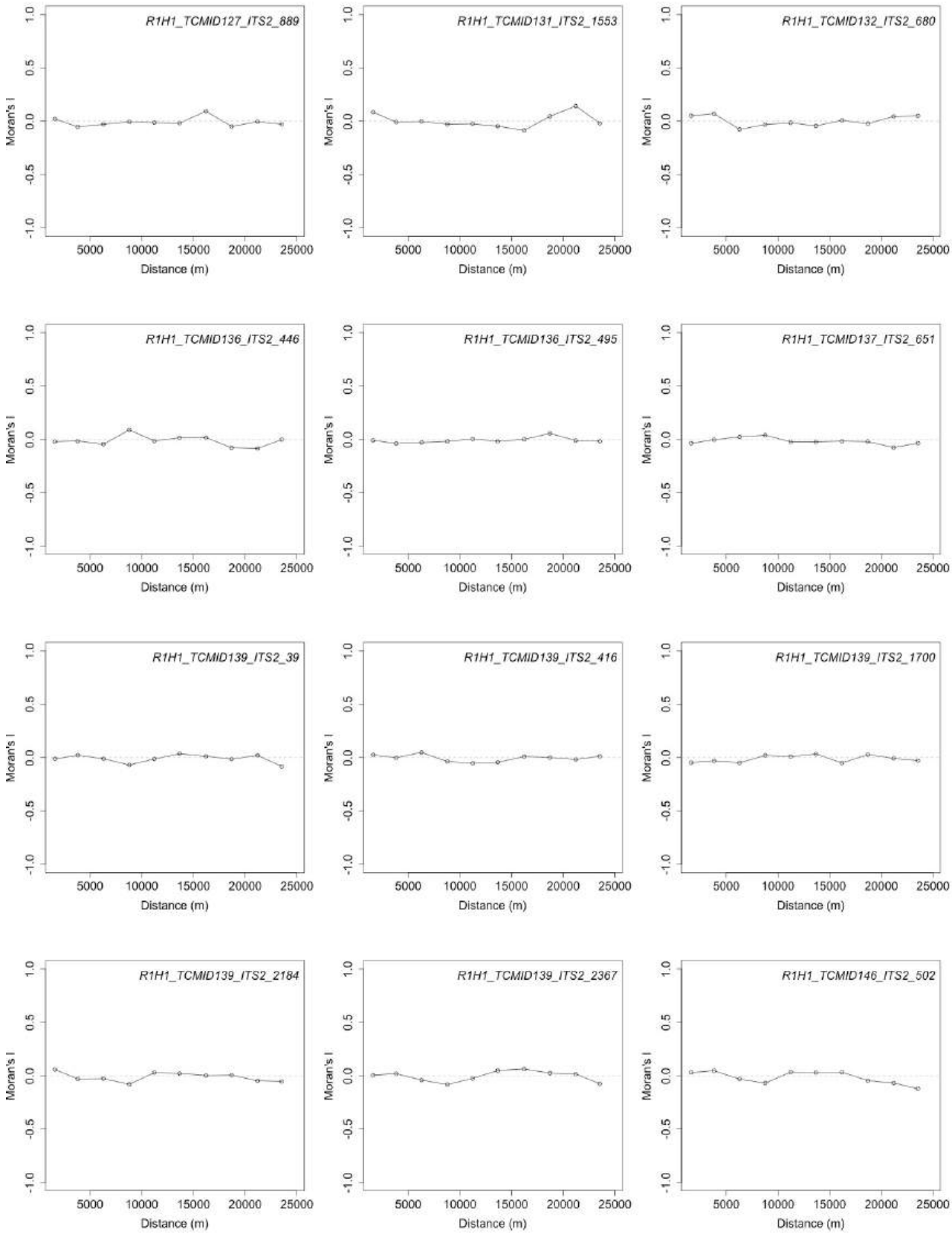
661 correlograms (cont.).



662

663 **Figure S6** Spatial autocorrelation of each species of the *Fungi* group based on Moran's *I* spatial

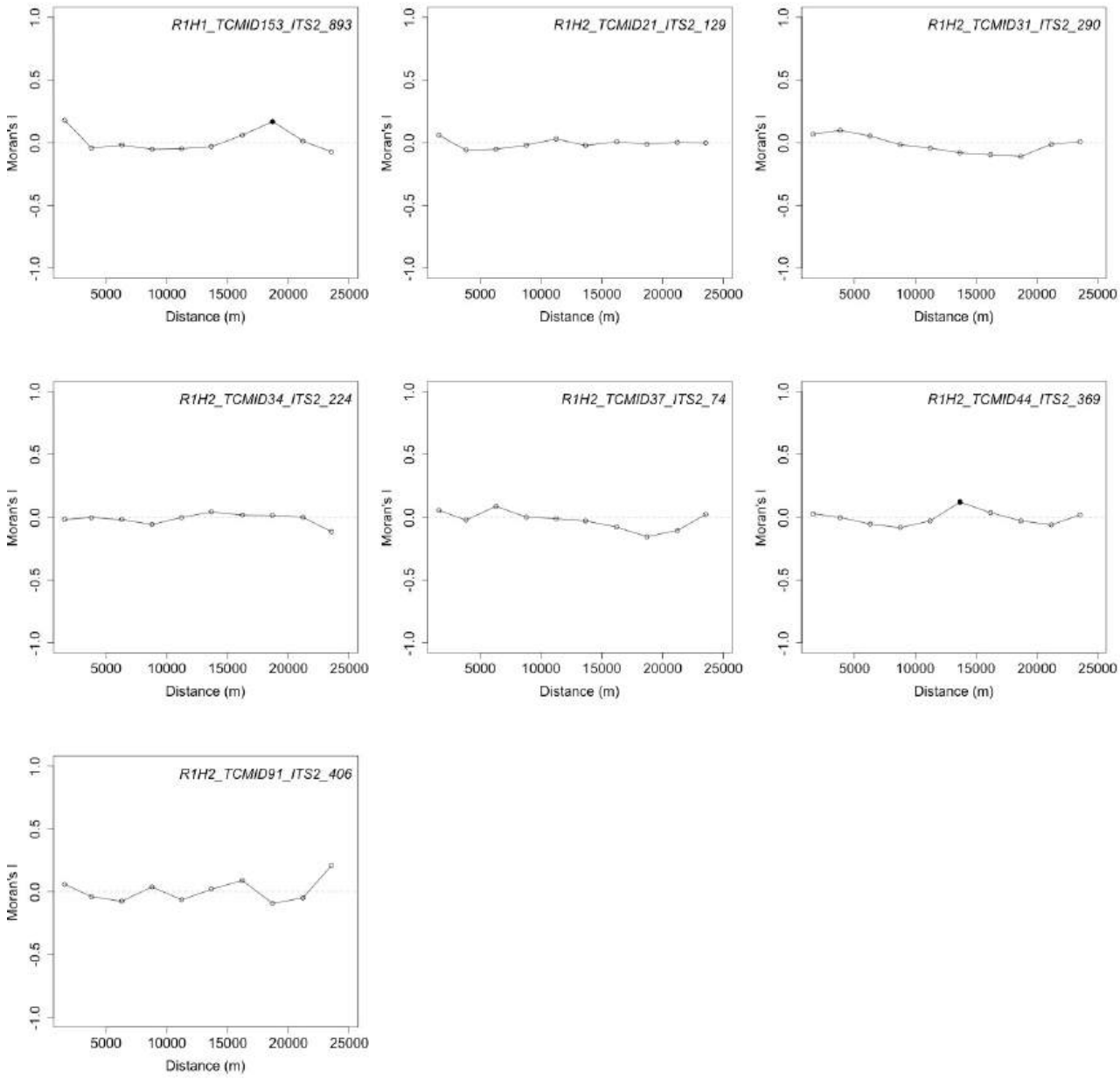
664 correlograms (cont.).



665

666 **Figure S6** Spatial autocorrelation of each species of the *Fungi* group based on Moran's *I* spatial

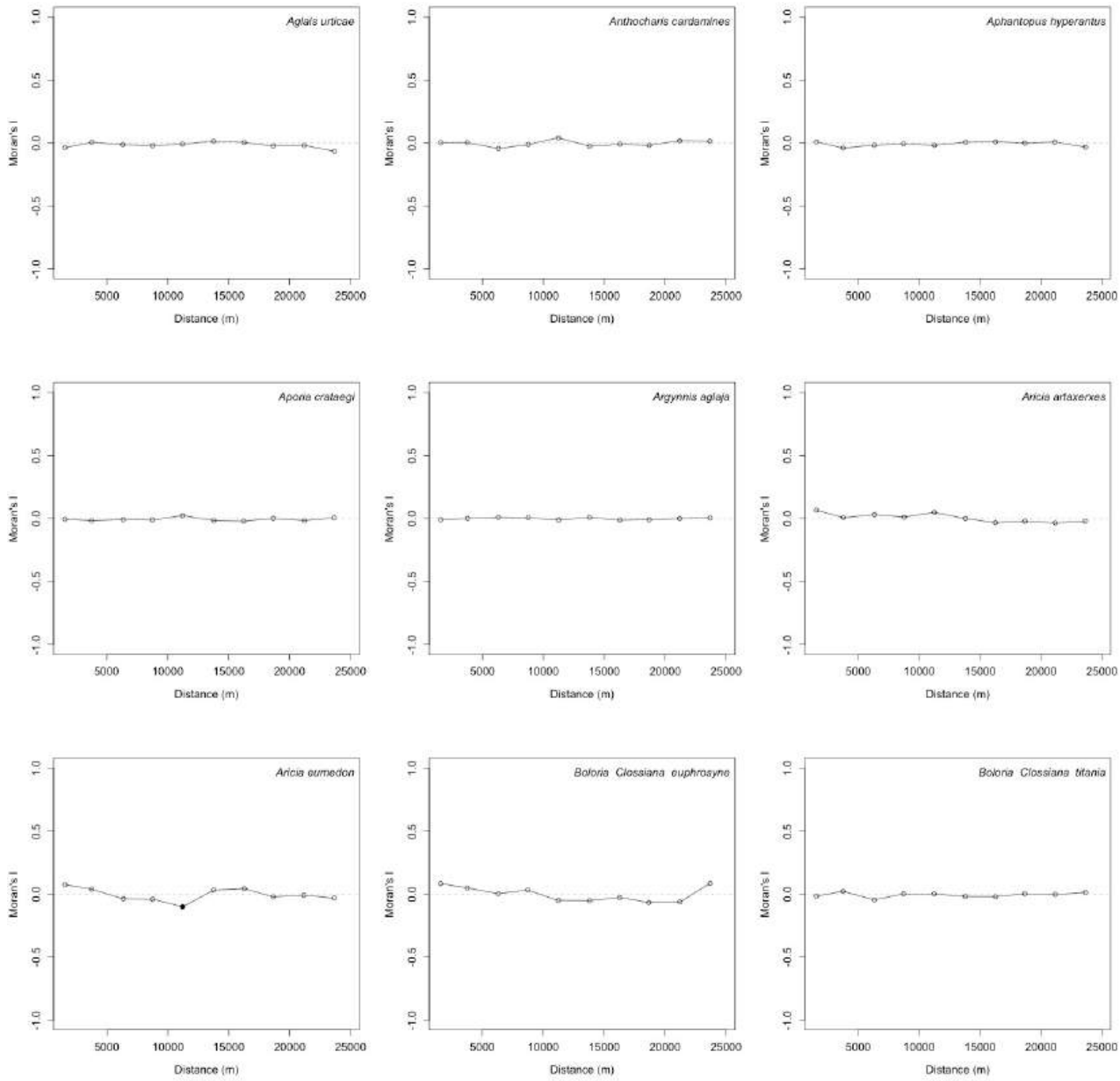
667 correlograms (cont.).



668

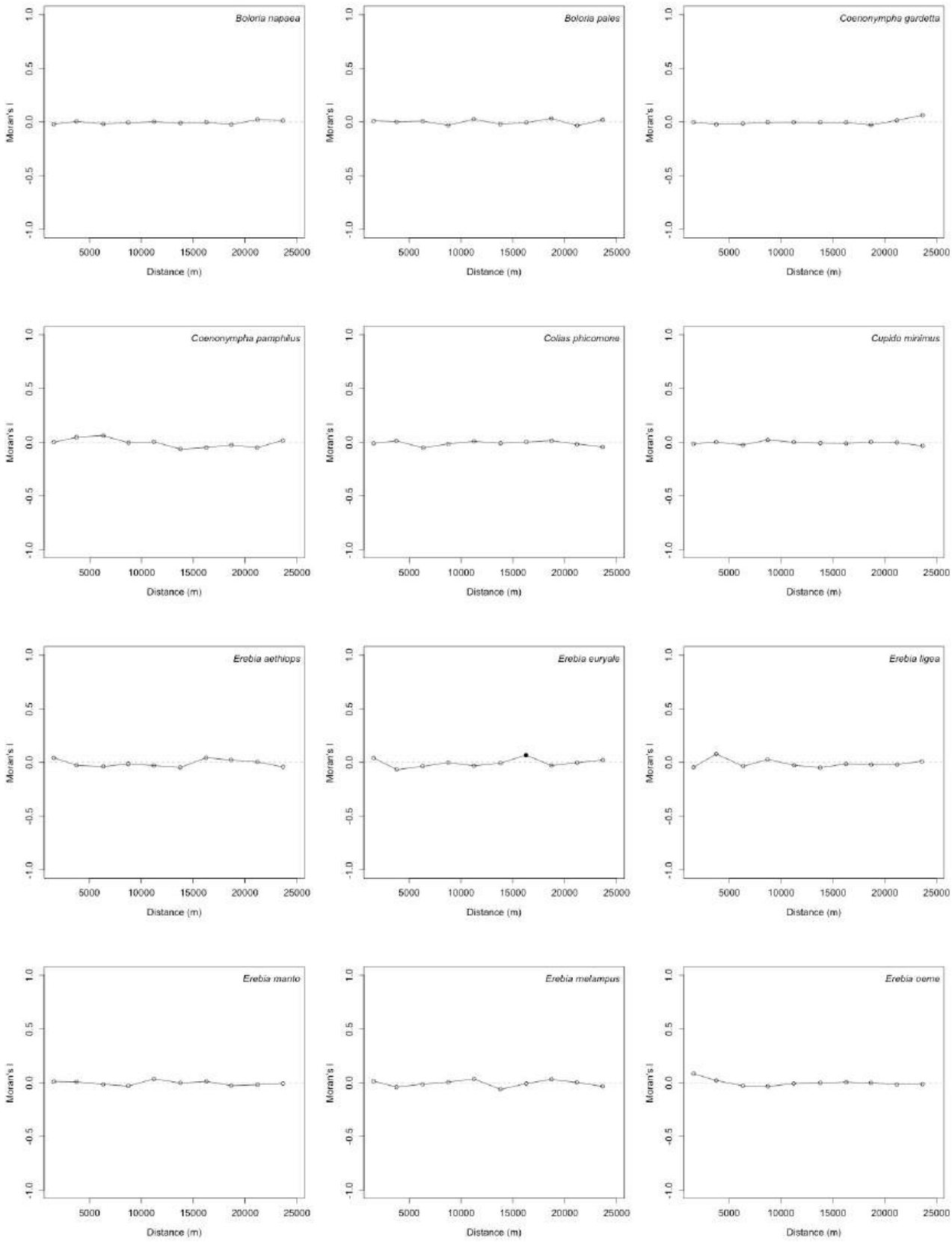
669 **Figure S6** Spatial autocorrelation of each species of the *Fungi* group based on Moran's *I* spatial

670 correlograms (cont.).



671

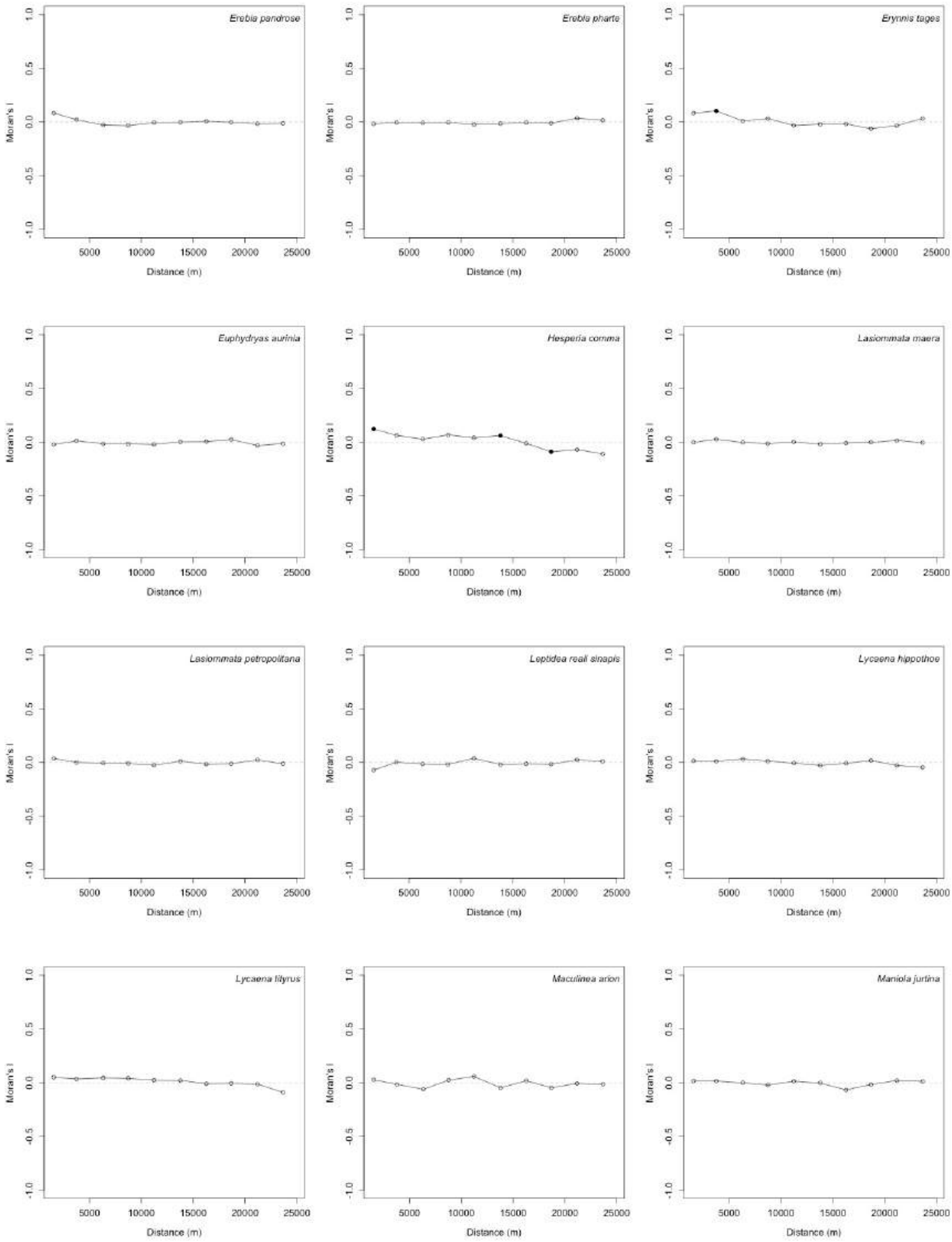
672 **Figure S7** Spatial autocorrelation of the models' residuals of each species of the *Lepidoptera* group based
673 on Moran's *I* spatial correlograms. All correlograms are globally significant at the α = 0.05 level since several
674 individual values are significant after Bonferroni correction. Filled symbols are significant values after
675 Holm's correction for multiple testing (α=0.05). Distances up to 2/3 of the maximum distance between two
676 observations are represented.



677

678 **Figure S7** Spatial autocorrelation of the models' residuals of each species of the *Lepidoptera* group based

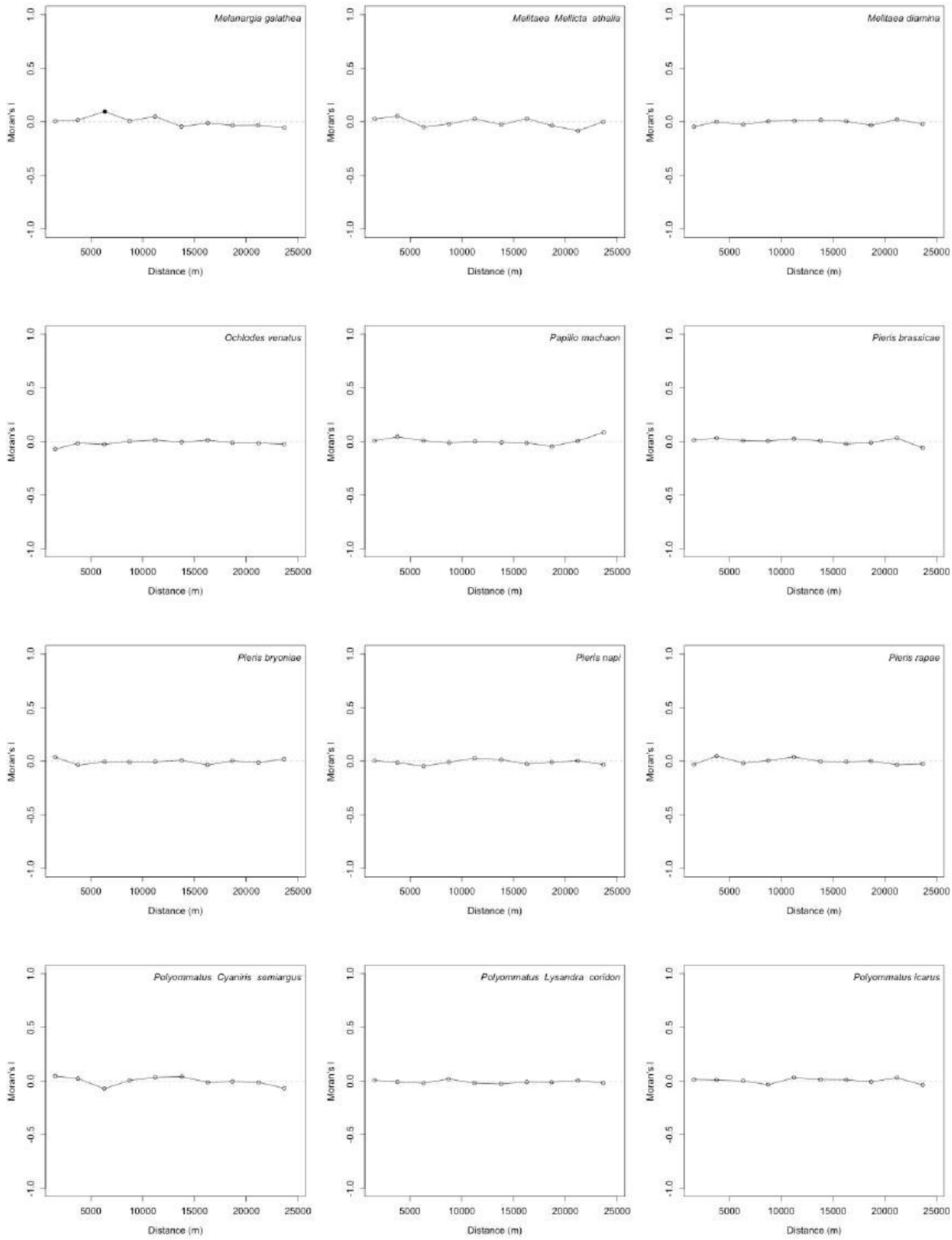
679 on Moran's *I* spatial correlograms (cont.).



680

681 **Figure S7** Spatial autocorrelation of the models' residuals of each species of the *Lepidoptera* group based

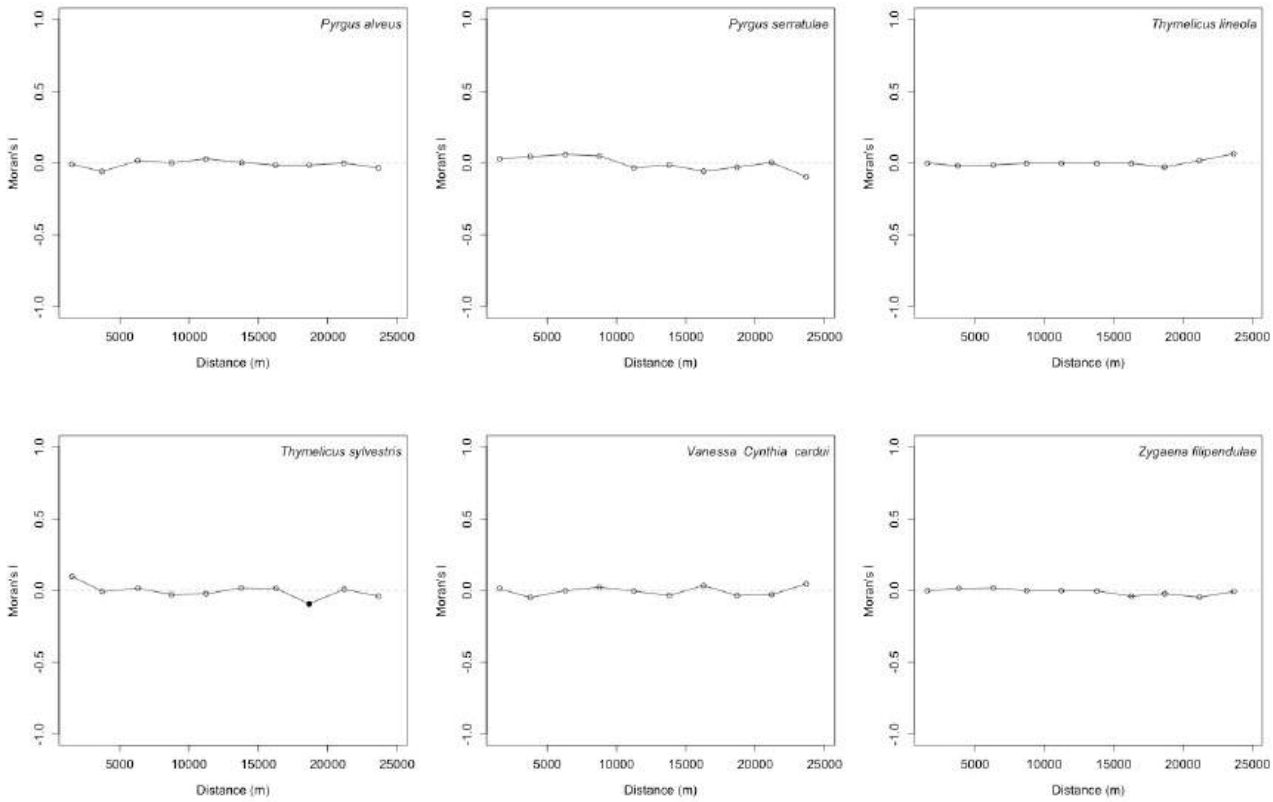
682 on Moran's *I* spatial correlograms (cont.).



683

684 **Figure S7** Spatial autocorrelation of the models' residuals of each species of the *Lepidoptera* group based

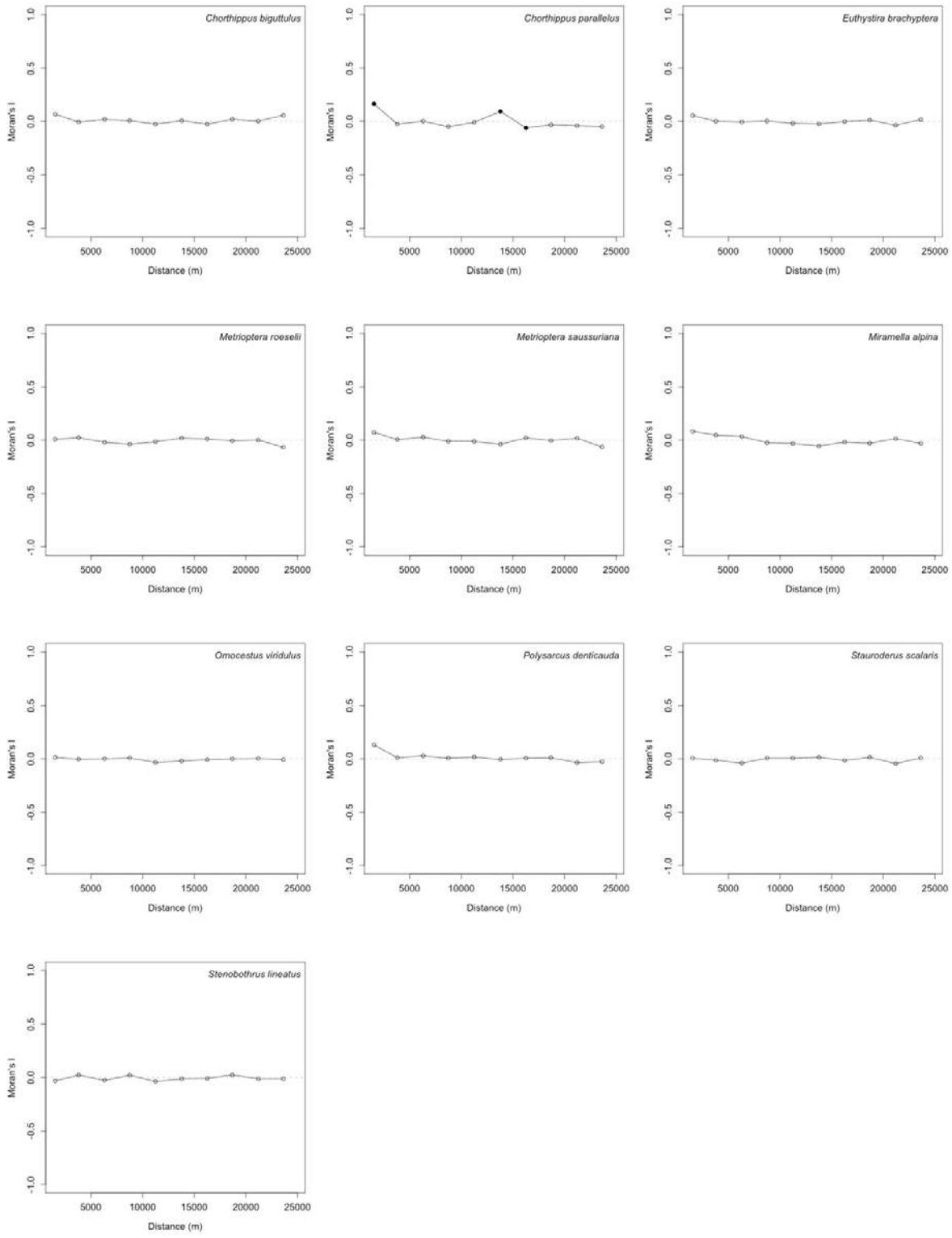
685 on Moran's *I* spatial correlograms (cont.).



686

687 **Figure S7** Spatial autocorrelation of the models' residuals of each species of the *Lepidoptera* group based

688 on Moran's *I* spatial correlograms (cont.).



689

690 **Figure S8** Spatial autocorrelation of the models' residuals of each species of the *Orthoptera* group based on
691 Moran's *I* spatial correlograms. All correlograms are globally significant at the α = 0.05 level since several
692 individual values are significant after Bonferroni correction. Filled symbols are significant values after
693 Holm's correction for multiple testing (α=0.05). Distances up to 2/3 of the maximum distance between two
694 observations are represented.