Differential effects of exotic Eurasian wild pigs and native peccaries on physical integrity of streams in the Brazilian Atlantic Forest

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Abstract

Wild boars (Sus scrofa Linnaeus, 1758), native to Eurasia and Africa, are one of the world’s most widely distributed invasive species. Their impacts on terrestrial environments have been well documented, however little is known about their effects on aquatic environments. We used standardized physical habitat surveys to compare the use of streams by invasive wild pig and native white-lipped peccaries (Tayassu pecari Link, 1795), and their effects on the physical structure from four first-order streams in the Brazilian Atlantic Forest. Two of these streams were used solely by wild pigs, while two were solely used by peccaries. Each stream was subdivided by cross-sectional transects into continuous sections, each 10-m in length, where we measured the intensity of use by each species and different variables related to the stream physical habitat. Although both species used the streams, wild pigs altered physical and environmental parameters more, and with greater intensity, than the native peccaries. Wild pigs decreased the stream bank angle and the riparian ground cover, leading to local erosion, increased fine sedimentation and wetted width, and declined stream depth. We recommend studies to evaluate the biological consequences of the alterations caused by introduced wild pigs, which should be conducted along with plans of population control in environments where the wild pig is considered an invasive species.

Key words: Sus scrofa, Tayassu pecari, ecosystem engineer, feral hogs, wild boar

Introduction

The physical and chemical features of streams are good indicators of stream ecological integrity and their biological condition (Casatti et al. 2006). Activities which disrupt stream physical structure may affect aquatic biodiversity and ecosystem processes (Gorman and Karr 1978; Resh et al. 1988). Anthropogenic land use change causes most of the disruptions in stream physical habitat characteristics (e.g. Wang et al. 2003; Kaufmann and Hughes 2006). However, other organisms can also disrupt the habitat of streams and affect aquatic community structure (Meysman et al. 2006). Particularly in fresh water systems, various vertebrates, called "ecosystem
engineers” (Jones et al. 1994), can promote alterations in physical habitats and water quality, including native (e.g. Peterson and Foote 2000; Tiegs et al. 2009; Hogg et al. 2014) and introduced fish species (e.g. Bain 1993), and mammals (Butler and Malanson 1995; Coronato et al. 2003; Anderson and Rosemond 2007; Beck et al. 2010; Doupé et al. 2010).

The use of streams by exotic species can result in alterations with negative consequences for the environment due to the disruption of trophic dynamics, habitat structure, and/or the frequency and intensity of disturbances and geochemical cycles (Simberloff 2011). The wild pigs (Sus scrofa), native to Eurasia and northwestern Africa (Long 2003), are one of the oldest species intentionally introduced by humans (Courchamp et al. 2003; Long 2003). They are recognized as an important alien ecosystem engineer, changing the soil structure (Singer et al. 1981; Cuevas et al. 2012), vegetation cover by suppression of native species (Barrios-Garcia and Ballari 2012; Cuevas et al. 2012), causing alteration in the structure of the seed bank (Ickes et al. 2001; Bueno et al. 2011) and the spread of exotic grasses (Sanguinetti and Kitzberger 2010; Dovrat et al. 2012). The disruption of habitats and nests caused by wild pigs leads to reduction of abundance and richness of vertebrates and invertebrates that depend on the soil, litter and shrub-herbaceous stratum as habitat (Singer et al. 1984; Barrios-Garcia and Ballari 2012). Wild pigs also prey on soil meso- and macrofauna (e.g. insect, larvae, earthworms, beetles, etc.), vertebrates and eggs. The effects of wild pigs on native fauna can lead to cascading effects on ecosystem processes that are still unknown (Barrios-Garcia and Ballari 2012).

There is no consensus about the effects of wild pigs on aquatic environments. Doupé et al. (2010) reported negative changes in the aquatic plant community and water quality, while Arrington et al. (1999) observed an increase in the aquatic plant diversity in water bodies used by wild pigs. Therefore, their foraging behavior, which consists of rooting (Barrios-Garcia and Ballari 2012), and their need for body temperature regulation, promotes the formation of large bogs in water bodies (Barrett 1978; Coblentz and Baber 1987; Cuevas et al. 2013).

In the Neotropics, the white-lipped peccary (Tayassu pecari)—that can be considered the native ecological equivalent of the wild pig in those regions (Novillo and Ojeda 2008)—can modify streams and create microhabitats for amphibians (Beck et al. 2010). The white-lipped peccary is one of the largest Neotropical mammals (Fragoso 1999) and in their natural range the populations are declining due to habitat fragmentation and poaching (Reyna-Hurtado 2009, Reyna-Hurtado et al. 2010; Altrichter et al. 2012). However, unlike wild pigs, the white-lipped peccary does not seem to have become a problematic invasive species where it has been introduced (Mayer and Wetzel 1987).

Wild pigs are distributed throughout Brazil, but mainly concentrated in the Brazilian Atlantic Forest Biome (Pedrosa et al. 2015; Rosa et al. 2017).
The Serra da Mantiqueira is a mountain range extending for 500 km along southeastern Brazil and one of the more important areas of the Brazilian Atlantic Forest Biome, considered to be an area of global importance for biodiversity conservation (Myers et al. 2000; Le Saout et al. 2013). According to local residents, in 2006, six pigs that had been kept enclosed on a commercial breeding site, were intentionally introduced next to Itatiaia National Park (INP), one of the largest protected areas of the Serra da Mantiqueira. These pigs established feral populations one of which in the Serra da Mantiqueira estimated at 199 (SD = 1.38) individuals with a density of 15,8 ind./km² (Puertas 2015) and no control effort have been made.

Both the wild pig and white-lipped peccary use streams in their daily activities and have rooting and wallowing behavior and the potential to alter the stream physical habitat structure of streams (Arrington et al. 1999; Beck et al. 2010; Doupé et al. 2010). To better understand the potential effect of wild pigs on aquatic environments of Brazilian Atlantic Forest, we compared the use of streams by the alien wild pig and the native white-lipped peccary and their consequences on the physical structure of first-order streams. We hypothesized that stream use by wild pigs has a potential to disrupt the physical structure of streams more intensely than its use by white-lipped peccaries.

Materials and methods

Study Area

The Itatiaia National Park (INP) is the most representative of a patchwork of protected areas in the Serra da Mantiqueira. The INP can be divided into two main regions according to their altitudinal range. The Lower Part (LP) (22°26′14″S; 44°36′3″W) have lower altitudes varying between 600 and 1,500 m and a Cfb mesothermal climate type (Köppen 1936). The Higher Part (HP) (22°20′23″S; 44°43′17″W) is a region with elevations between 1,500 and 2,791 m, and a mesothermal Cwb climate type (Köppen 1936). Both these regions have dry season in winter and a rainy season in summer. The INP is covered by montane forest and high altitude grasslands, with predominance of Araucaria tree (Araucaria angustifolia) in HP and palm tree (Euterpe edulis) in LP. Both tree species are considered a key resource for the fauna groups of the Park, including wild pigs and peccaries (Iob and Vieira 2008; Genini et al. 2009; Ribeiro and Vieira 2014). The area covered by INP has 12 important regional watersheds that drain into two main basins: the Grande River, a tributary of the Paraná River, and the Paraíba do Sul River.

Between 2013 and 2016 we have conducted a continuous monitoring program of mammal activities in our study area with automatic cameras, which provided no evidence of sympatry between white-lipped peccary and wild pigs. The wild pig occurs only in the HP while the white-lipped...
peccary occurs only in the LP (Abreu 2016). Thus, we selected four headwater streams (first order); two in the LP areas and two in the HP areas (Figure 1). Their riparian vegetation cover were similarly represented by forest in advanced successional stage, with canopy height between 15 and 20 meters.

**Data Collection**

To determine the use of streams by wild pigs and peccaries and the consequences on the physical structure of first-order streams, we carried out an observational study during the dry season between October and November 2013. For this, we performed a standardized physical habitat survey adapted from the previous methodologies that used physical, chemical
and biological variables to assess the integrity of streams (Peck et al. 2006; Hughes and Peck 2008).

We surveyed four streams used by the native and introduced pig species; two in the LP area (with peccaries and without wild pigs) and two in the HP area (with wild pigs and without peccaries) (Figure 1). To ensure independence between our sampling units when evaluating the physical characteristics of streams, we subdivided each stream by cross-sectional transects into continuous sections of 10 m in length each (Figure 2); as recommended by Peck et al. (2006) and Hughes and Peck (2008). Both species occurred over the area sampled, thus we could not find streams that are not used by at least one species in all their extension. However, we did find stream sections with different use intensities (e.g., footprints, rooting, see Engeman et al. 2013), or even without evidence of use by the pig species. To set the control points and evaluate how different use intensities of species can alter the physical integrity of streams, we employed an intensity score from the presence or absence of footprints and rooting every 1 meter in each 10 m section. Each 1 meter accounted for 10% of the total 10 m section, resulting in a use intensity ranging from 0 to 100% in each 10 m section (Figure 2). The control sections were those in which the intensity scores were 0%. All the streams had along their studied courses the same riparian cover and gradient (slope), which are considered the most important drivers of the measured physical characteristics (Peck et al. 2006). Therefore, such aspects were important to assure that the physical characteristics of the preferred sections are a consequence of rooting and wallowing activities, and not the reason why these sections were selected.

In total, we measured in 16 sections used by wild pigs and 12 control sections in HP, and in 13 sections used by white-lipped peccaries and 24 control sections in LP. Field experiments were approved by the Research
To measure the effects from use intensity on stream conditions in each 10m-section, we measured physical variables associated with morphology and type of substrate of streams that could be altered by ecological engineers (such as wild pigs and peccaries from previous field observations). At each of the cross-sectional transects we measured depth (DEPTH) and visually examined substrate type (bedrock, concrete, boulders, cobbles, coarse gravel, fine gravel, sand, silt and clay, hardpan, fine litter, coarse litter, wood, roots) along five equidistant points. Based on substrate type we calculated the mean substrate diameter (SIZE_CLS), the percentage of substrate smaller than fine gravel (SEDIMENT), and larger than boulder (LARGER). Transect characterization also included bank width (BANKWID), mean wetted width (WT_WID), undercut bank distance (UNDERCUT), and bank angle (ANGLE). We assessed habitat complexity at each transect in 10 m length plots inside the stream channel, using semi-quantitative visual estimates (%) of the surface cover of leaf packs, roots, large woody debris > 30 cm diameter, brush and small woody debris, overhanging vegetation < 1 m above the water surface, undercut banks, boulders, and artificial structures. These variables were used to estimate the number of woody debris pieces (PIECES), riparian ground cover (RIP_GC) and shelter for aquatic organisms (SHELTER).

Data Analysis

Despite the climate and orography difference between the Lower Part (LP) and the Higher Part (HP) of this National Park, the streams we studied are all located at the same biome domain and geological background. However, our analyses focused on local comparisons to cope with the differences between the two regions. In this way, our controls sections are local, what means that control sections of the HP are the sections located in HP and the control sections of the LP are the sections located in LP. We divided the sampled sections into four groups: (1) points in HP not used by wild pigs (control points); (2) points in the HP used by wild pings; (3) points in LP not used by peccaries (control points); and (4) points in LP used by peccaries. The variables describing the stream conditions were examined using principal component analysis (PCA). Differences among the four groups were tested by discriminant correspondence analysis (DCA) using the software Statistica 6 (StatSoft Inc. 2001).

We tested the normality distribution of the variables from each stream by using the Shapiro-Wilk test and compared the mean values between the groups of sampled sections (groups 1 and 2, and between groups 3 and 4), using the Kruskal-Wallis test for non-normal data, and the Student’s t-test for normal data using the software Bioestat 5.0 (Ayres et al. 2007).
Figure 3. PCA showing the effects of *Sus scrofa* (in black) and *Tayassu pecari* (in gray) in the sampled points. Black crosses indicate the control points of *Sus scrofa* area (Group 1); black balls indicate points used by *Sus scrofa* (Group 2); Gray crosses indicate the control points of *Tayassu pecari* area (Group 3); gray balls indicate points used by *Tayassu pecari* (Group 4). The bubbles represent the use intensity (%) of each species, where the larger the ball, the higher the use intensity of the species.

**Results**

We found significant differences of stream physical characteristics in sampled sections used by wild pigs and peccaries. When ordered, these differences were most evident along the first axis of the PCA (Figure 3). In general, both species were associated with shallower stream depths, and replacement of the larger substrate by fine gravel (Table 1). However, while all sections with any intensity of use by wild pigs showed these characteristics, only those with high values by peccaries (> 50% of use intensity) followed this pattern. In sections used by wild pigs, stream characteristics related to the second axis of the PCA were altered (Figure 3), in particular by reducing the undercut bank distance (Table 1).

When evaluated on its own set of variables, the four groups differed (p < 0.05), mainly due to the amount of larger substrate (LARGER) and riparian ground cover (RIP_GC) (Table 2). In stream sections used by either species, we noted the cover of large substrate by silt and removal of riparian ground cover.
Table 1. Stream attributes, PCA scores and contribution to the first three PCA components of the variables measured in streams used by *Tayassu pecari* and *Sus scrofa*. Highest scores of each axis are in bold and scores between −0.3 and 0.3 are presented only with a positive or negative sign.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PCA 1</th>
<th>PCA 2</th>
<th>PCA 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>DEPTH</td>
<td>0.74</td>
<td>−</td>
<td>−0.31</td>
</tr>
<tr>
<td>SIZE_CLS</td>
<td>0.46</td>
<td>0.39</td>
<td>0.32</td>
</tr>
<tr>
<td>SEDIMENT</td>
<td>−0.71</td>
<td>+</td>
<td>−0.52</td>
</tr>
<tr>
<td>ANGLE</td>
<td>0.64</td>
<td>0.32</td>
<td>−</td>
</tr>
<tr>
<td>WT_WID</td>
<td>0.51</td>
<td>−0.44</td>
<td>−0.49</td>
</tr>
<tr>
<td>BANKWID</td>
<td>−</td>
<td>−0.69</td>
<td>−0.32</td>
</tr>
<tr>
<td>SHELTER</td>
<td>0.48</td>
<td>0.30</td>
<td>−0.57</td>
</tr>
<tr>
<td>PIECES</td>
<td>−0.51</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>RIP_GC</td>
<td>0.69</td>
<td>−0.41</td>
<td>+</td>
</tr>
<tr>
<td>UNDERCUT</td>
<td>+</td>
<td>0.77</td>
<td>−</td>
</tr>
<tr>
<td>LARGER</td>
<td>0.83</td>
<td>−0.19</td>
<td>+</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>3.63</td>
<td>1.91</td>
<td>1.34</td>
</tr>
<tr>
<td>Variance explained (%)</td>
<td>32.99</td>
<td>17.33</td>
<td>12.14</td>
</tr>
<tr>
<td>Cumulative variance (%)</td>
<td>32.99</td>
<td>50.31</td>
<td>62.45</td>
</tr>
</tbody>
</table>

Table 2. F and exit values of the model and tolerance of the discriminant correspondence analysis, and p value for variance analysis of variables measured in streams used by *Tayassu pecari* and *Sus scrofa*.

<table>
<thead>
<tr>
<th>Variable</th>
<th>F-exit</th>
<th>Tolerance</th>
<th>P (DCA)</th>
<th>P (variance)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DEPTH</td>
<td>1.30</td>
<td>0.65</td>
<td>0.2844</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>SIZE_CLS</td>
<td>2.13</td>
<td>0.67</td>
<td>0.1082</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>SEDIMENT</td>
<td>1.83</td>
<td>0.60</td>
<td>0.1530</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>ANGLE</td>
<td>1.99</td>
<td>0.71</td>
<td>0.1267</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>WT_WID</td>
<td>1.39</td>
<td>0.57</td>
<td>0.2560</td>
<td>0.0395</td>
</tr>
<tr>
<td>BANKWID</td>
<td>2.31</td>
<td>0.53</td>
<td>0.0877</td>
<td>0.0218</td>
</tr>
<tr>
<td>SHELTER</td>
<td>1.76</td>
<td>0.60</td>
<td>0.1657</td>
<td>0.0152</td>
</tr>
<tr>
<td>PIECES</td>
<td>0.50</td>
<td>0.82</td>
<td>0.6823</td>
<td>0.0158</td>
</tr>
<tr>
<td>RIP_GC</td>
<td>3.03</td>
<td>0.68</td>
<td><strong>0.0378</strong></td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>UNDERCUT</td>
<td>0.44</td>
<td>0.65</td>
<td>0.7237</td>
<td>0.2260</td>
</tr>
<tr>
<td>LARGER</td>
<td>6.63</td>
<td>0.76</td>
<td><strong>0.0007</strong></td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

In sections used by wild pig the bank distance (UNDERCUT), mean wetted width (WT_WID), woody debris pieces (PIECES) and shelter (SHELTER), did not differ between control and streams-section used by species (Figure 4C, F). However, bank angle (ANGLE), sediment larger than boulder (LARGER), riparian ground cover (RIP_GC), mean substrate diameter (SIZE_CLS), fine gravel (SEDIMENT) and bank full width (BANKWID) were altered (Figure 4A, B, D, E, G). In areas were white-lipped peccaries occurred, bank distance (UNDERCUT), mean wetted width (WT_WID), woody debris pieces (PIECES) and shelter (SHELTER), also did not differ between control and stream sections used by species (Figure 4C, F). However, bank angle (ANGLE), sediment larger than boulder (LARGER), depth (DEPTH) and riparian ground cover (RIP_GC) were altered (Figure 4D, E, G, H).

**Discussion**

In sections used by wild pigs or peccaries, the physical structures of streams were altered. The main effect included decreasing stream depth by
Differential effects of wild pigs and peccaries on streams

Figure 4. Mean, standard deviation and maximum and minimum values of the physical streams variables measured in the sampled streams (1) control points of Sus scrofa area; (2) points used by Sus scrofa; (3) control points of Tayassu pecari area; (4) points used by Tayassu pecari. Different letters indicate significant differences (P < 0.05), with a and b representing the Groups 1 and 2 and c and d for Groups 3 and 4.

sedimentation due to replacement of the larger substrate by fine gravel. The fact that both species are associated with fine sediments could indicate a higher presence of these species in such habitat. However, since our control sections presented larger substrates and the sections with predominance of smallest substrates size were always associated with the bank collapse, these section features must be related to the use by one of the two species.
Even with abundance six times lower than white-lipped peccaries (Rosa et al., unpublished results), any intensity of use of streams by wild pigs caused bank erosion, reflecting also a decrease of the stream bank angle and the riparian ground cover. These results support our hypothesis that wild pigs change the physical structure of streams more intensely than peccaries, characterizing them as an agent of alien disturbance to the aquatic ecosystem of the Brazilian Atlantic Forest.

Significant effects of wild pigs on the physical structure of the soil, leaf litter, seed and land plants in terrestrial environments have previously been reported (e.g. Bueno et al. 2011; Wirthner et al. 2011; Cuevas et al. 2012). Their rooting behavior makes the soil less compact and wetter, which reduces the vegetative cover and, consequently, makes the soil more susceptible to wind erosion (Cuevas et al. 2012). Such rooting can also reduce ground vegetative cover and leaf litter, which in turn eliminates the presence of some small mammal species that are dependent upon those microhabitat parameters of the forest floor for their survival (Singer et al. 1984); and may lead to negative consequences for nutrient cycling processes in the soil.

We found no studies that had evaluated the use of wild pigs or white-lipped peccaries and their effects on stream physical habitats structure. However, Beck et al. (2010) showed that pools created and maintained by white-lipped peccaries are wider and hydrologically more stable over time than other pools, especially during times of drought, increasing the diversity of anurans. For wild pigs, Doupé et al. (2010) noted increased turbidity, changes in chemical composition and reduction of macrophyte coverage on an ephemeral flood plain lagoon used by this species. Arrington et al. (1999) did not assess the effect of wild pigs on the physical structure of wetlands, but noted increased vegetation in these areas due to the creation of microhabitats by this species. These authors point out that because of the wet ground, the ability of wild pigs to modify wetlands in wet periods is limited, providing an opportunity for the vegetation to recover, leading to an increase in plant species diversity in these areas.

In the terrestrial environment, wild pigs root and graze to a greater extent than the peccaries, what is likely because of their differences in cranial anatomy (Ilse and Hellgren 1995; Sicuro and Oliveira 2002). In the Brazilian Pantanal, where peccaries and wild pigs coexist, skull morphological differences between these species have been related to a higher soil rooting performance by the wild pigs that allows soil excavation up to 50 times deeper those by peccaries (Sicuro and Oliveira 2002). We believe that these same cranial differences can have a relation to the wild pig’s ability to modify aquatic environments more than the peccaries.

Where it is an invasive species, the wild pig facilities invasions, creating new habitats for exotic species thus increasing their richness and
abundance (Kotanen 1995; Cushman et al. 2004). However, where it is native, it is possible to observe resiliency in the native herbaceous plant community, probably due to their mutual evolutionary history (Dovrat et al. 2014). The same occurs with the white-lipped peccary through its wallowing behavior, which creates pools that are used for reproduction by different frog species, leading to an increased density and diversity of frogs in the Peruvian Amazon (Beck et al. 2010).

Native or exotic ecosystem engineers can alter the frequency regime of disturbances (e.g., grazing and fire), as well as being the source of disturbance itself (Crooks 2002), and this may increase the alpha (Arrington et al. 1999) and beta diversity (Astorga et al. 2014). Thus, the effects of ecosystem engineers are a matter of scale and context, depending on the landscape and the regional species pool in which the activity is brought about. The effects on species diversity vary depending on the scale of influence on the resource and its influence on the increase or decrease in diversity as the heterogeneity is reduced or increased (Crooks 2002). Thus, the ecosystem engineers may be crucial for maintaining biodiversity in some landscapes, especially those where the disturbance regime and frequency have been altered due to other human activities (Badano and Cavieres 2006).

In the case of wild pigs, our study indicates that the presence of an exotic ecosystem engineer modifies the physical structure of streams; however, we do not know the ultimate consequences. Although the disturbance can increase the number of habitats, we must remember that in tropical environments heterogeneity of substrates is critical for fish diversity, including sympatric congeneres (Leal et al. 2010), and we do not know the consequences of stream physical habitat changes caused by wild pigs on fish and other aquatic organisms.

The Itatiaia National Park is recognized as a fundamental area for water resources and biodiversity preservation, but suffers with domestic and exotic species such as wild pigs, feral dogs, cattle and domestic horses – whose synergy can enhance the impact of each species individually (Simberloff 2011). As an immediate solution to reduce the effects of wild pigs on streams is to fence streams, something that has already proved to be successful in Australia (Doupé et al. 2010). However, without a wild pig population control program, the fencing of streams would be just a palliative solution.

Wild pigs are among the 100 worst invasive species in the world (Lowe et al. 2000). Due to their high potential to negatively affect native habitats and biota, the precautionary principle encourages action to be taken to control or even eradicate this potentially harmful alien species as soon as they are detected, even if their impacts and the ecosystem resilience have not been quantified at the local scale (Wittenberg and Cock 2001). Brazilian law results in great limitations for wildlife management strategies, mainly regarding the lethal control of populations. Recently, wild pigs were...
recognized as a risk for the Brazilian economy and biodiversity; because of that their population control by hunting and live-traps has been allowed (Instrução Normativa Ibama 03/2013), and can be done by any licensed Brazilian citizen. Therefore, we recommend that Protected Areas include the control of this invasive exotic species in their management plans, and that the control techniques and management of exotic species need to be extended to the surrounding areas, also strategically conducted in conjunction with the local human populations.

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References

Abreu TCK (2016) O javali (Sus scrofa) na Serra da Mantiqueira: ocupação e distribuição em áreas de proteção ambiental. Master Dissertation, Universidade Federal de Lavras, Lavras, Brazil, 42 pp


Köppen W (1936) Das geographisca System der Klimate. In: Köppen W, G e i g e r R (eds), Landscape influences on stream habitat and biological assemblages. American Fisheries Society, Symposium 48, Maryland, EUA, pp 429–455

Köppen W (1936) Das geographisca System der Klimate. In: Köppen W, G e i g e r R (eds), Landscape influences on stream habitat and biological assemblages. American Fisheries Society, Symposium 48, Maryland, EUA, pp 429–455

Klimatologie. Gebr, Borntraeger, Germany, pp 1–44


Long JL (2003) Introduced mammals of the world: their history distribution and influence, CSIRO, Collingwood, Australia, 612 pp

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the World’s worst invasive Alien species a selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), Gland, 11 pp


